On the evolutionary morphology of the mammalian neck: Disparity and constraints

Dissertation

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“The neck may have evolved to perform several functions at once.”

The tallest Tale, 1996

Stephen J. Gould, paleontologist & evolutionary biologist

Content

Chapter 1

General Introduction

From Lamarck's giraffes to developmental constraints

The remarkable length of the neck of the giraffe is an example often used when describing the 'mechanics' of neck evolution in mammals, from illustrating the inheritance of acquired characteristics, as proposed by Jean-Baptiste de Lamarck (1809), to representing a microevolutionary adaptation as a result of sexual selection (Simmons and Scheepers 1996; Badlangana et al. 2009; Simmons and Altwegg 2010). It is not its enormous length in the giraffe, however, that makes the mammalian neck a gripping subject for evolutionary biologists but the conspicuous constancy in the number of its constituting vertebrae. The vertebral column in mammals consists of morphologically differentiated groups of vertebrae (Gaunt 1994; Burke et al. 1995): cervical, thoracic, lumbar, sacral, and caudal. Therein, the number of cervical vertebrae is (almost) constant at seven, irrespective of the neck length and body size of different species – long-necked giraffes and short necked whales, big elephants and tiny shrews all possess seven cervical vertebrae. Only the extant tree sloths (*Bradypus* and *Choloepus*) and the manatees (*Trichechus*) deviate from this pan-mammalian 'rule' (Owen 1853, 1866; Bateson 1894; Buchholtz and Stepien 2009; Varela-Lasheras et al. 2011; Buchholtz et al. 2014). The exceedingly low level of interspecific variation in the number of cervical vertebrae of mammals has puzzled biologists for nearly two centuries (Goethe 1817; Cuvier 1835; Owen 1853, 1866; Flower and Lydekker 1891; Remane 1936; Galis 1999; Narita and Kuratani 2005; Galis et al. 2006; Buchholtz et al. 2012). In birds and sauropods, the number of cervical vertebrae is highly variable (Owen 1853, 1866; Boas 1929; Taylor and Wedel 2013) and evolutionary variation in number has proven to be adaptive regarding avian neck functionality (Van Der Leeuw 1991).

However, functional diversity of the mammalian neck is as high as in birds, with numerous head-neck postures adopted during foraging, drinking, grooming, exploration, social interaction, and locomotion. It has only recently been revealed that meristic constancy in the mammalian cervical spine does not need functional-adaptionistic explanations but is based on developmental constraints (Galis 1999; Galis and Metz 2003; Narita and Kuratani 2005; Buchholtz et al. 2012).

Developmental Framework

The evolutionary origin of the fixation at seven cervical vertebrae in mammals is not yet fully understood. There are two main hypotheses that relate to two different developmental processes. The first hypothesis proposes that changes in the number of cervical vertebrae in mammals are coupled with a variety of congenital abnormalities and an increased susceptibility to cancer (Galis 1999; Galis and Metz 2003; Galis et al. 2006; Galis and Metz 2007). Cervical ribs on C7 are interpreted as homeotic changes in the cervico-thoracic boundary. They are frequently accompanied by anatomical abnormalities in human stillborns, especially regarding the development of the brachial plexus and the transitional zone between the lower neck and shoulder (Galis et al. 2006; Furtado et al. 2011). Thus, human data supports that pleiotropic constraints (Hansen and Houle 2004) are at the root of the evolutionary conservation of the number of cervical vertebrae in mammals (Fig. 1 left). It is proposed that the unavoidability of such pleiotropic effects is due to the strong interactions during the early developmental stage when the number of cervical vertebrae is determined (Galis et al. 2006). This determination happens as part of the early anterior-posterior patterning of the paraxial mesoderm, mediated by the well-known Hox genes (Kessel and Gruss 1991; Wellik and Capecchi 2003; Deschamps and van Nes 2005; Mallo et al. 2010). The strong interactivity during the determination of the number of cervical vertebrae supposedly leads to even more deleterious pleiotropic effects, resulting in strong prenatal selection of individuals with a changed number of cervical vertebrae (Galis and Metz 2003; Varela-Lasheras et al. 2011) (Fig. 1 left). Thus, changes in vertebral count are prohibited by strong negative selection.

In the second hypothesis, the fixation of the number of vertebrae is based on mesoderm patterning in the neck region and the evolutionary origin of the mammalian diaphragm (Buchholtz et al. 2012; Buchholtz 2014). While migratory muscle precursor cells from the lower neck contribute to the muscle of the forelimb, a novel somatic cell stream originating from the midcervical somites muscularizes the diaphragm in mammals.

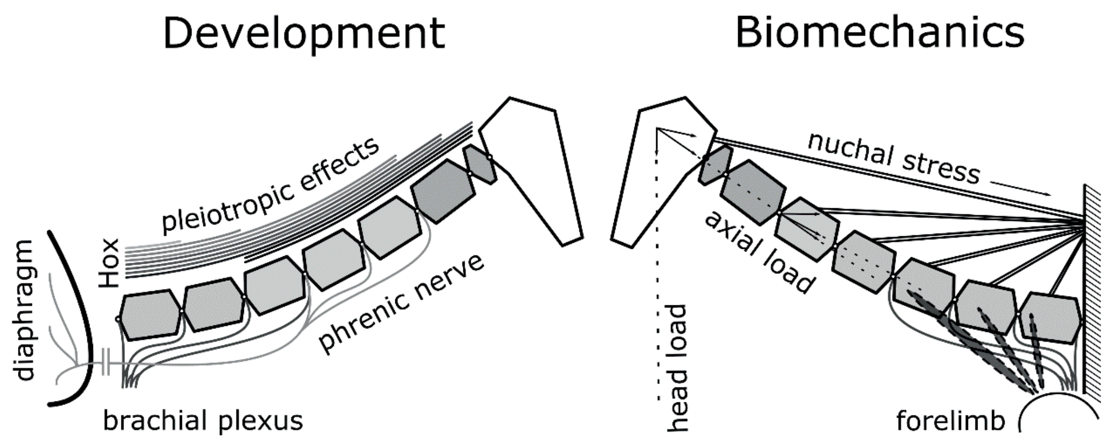

Figure 1 Developmental constraints (left) and biomechanical determinants (right) governing the general morphology of the mammalian neck. Simplified Hox gene pattern after Kessel and Gruss (1991). Biomechanical model adopted and modified after Kummer (1959a, 1959b).

In adults, the cervical origin of the diaphragm muscles is still recognizable in their innervation by the phrenic nerve (Greer et al. 1999; Birchmeier and Brohmann 2000; Babiuk et al. 2003) (Fig. 1 left). Buchholtz et al. (2012) propose a specialized midcervical region that provides the somatic origin of diaphragm muscles and the phrenic nerve. In contrast, the more caudal parts of the neck provide the somatic origin of forelimb muscles and the brachial plexus (Fig. 1 left). The strong developmental integration between the cervical submodules and other structures (head, forelimb, and diaphragm) places a strong constraint on variation in cervical organization by preventing meristic variability. This hypothesis is further supported by recent findings that evolutionary modifications at the head-trunk interface associated with migrating mesoderm cells are crucial for the general structuring of the trunk (Hirasawa and Kuratani 2013; Hirasawa et al. 2016). The fixation of the number of cervical vertebrae is therefore an evolutionary by-product of key innovations (muscularized diaphragm, thoraco-lumbal differentiation) in mammalian metabolic and locomotor performance (Buchholtz et al. 2012; Galis et al. 2014).

Although the two hypotheses cite different developmental processes to explain the fixation of the number of vertebrae, they are not mutually exclusive. Both agree that the stasis of the mammalian neck is based on a strong developmental integration between the neck and other body regions (either by the pleiotropic effects of cervical Hox genes or by emigrating somite derived cell streams). They may act in parallel but during different developmental stages and, in combination, strengthen the meristic limitations in the neck. Thus, the fixed cervical count is unrelated to the actual function of the neck as the main actuator of the head in space.

Biomechanical Determinants

In addition to the developmental constraints, biomechanical determinants govern the overall neck construction in mammals. The cervical spine constitutes a simple beam that is supported at one end only (i.e. cantilever or loaded beam construction; Kummer 1959a, b) (Fig. 1 right). The gravitational effect of the weight of the head at the unsupported end results in permanent stress (tension and compression) on the neck and the tendency of the head to collapse downward in an unbraced condition due to the bending moment (Martin et al. 1998). Unlike in birds and long necked sauropods, head/neck support in mammals is complicated by the efficient masticatory apparatus (e.g., extensive masticatory muscles). To counteract head bending and cervical stress, passive (nuchal and spinal ligaments) and active (dorsal neck muscles) elements stretch from the anterior trunk to the head and the cervical vertebrae and constitute the anterior part of the bow-and-string construction of the mammalian movement system (Zschokke 1892; Gray 1944; Slijper 1946; Kummer 1959a, b; Preuschoft 1976). As the nuchal elements completely compensate the head bending moment to allow the head and neck to maintain a static posture, the cervical vertebrae are purely under axial load (Kummer 1959a, b) (Fig. 1 right). This general construction limits variation in vertebral body shape and in the orientation of vertebral processes. Furthermore, it leads to the stereotypical vertical, s-shaped, and self-stabilizing resting posture of the mammalian cervical spine (Vidal et al. 1986; Graf et al. 1995b). Since head/neck movements start from this posture, orientation and changes in gaze in the sagittal plane are restricted to the cranio-cervical and the cervico-thoracic junctions. The mid-cervical spine does not contribute to the movement to any significant extent and the neck is thus functionally tripartite (Graf et al. 1995a; Graf et al. 1995b).

Paleontological Background

Shortly after the origin of amniotes, ‘reptilian’ lineages and synapsids evolved very different degrees of plasticity in their vertebral numbers. Basal synapsids shared the conserved axial configuration of crown mammals but basal reptiles already demonstrated the plasticity of extant taxa. (Müller et al. 2010). Accordingly, there was a clear divergence in axial, and thus cervical, developmental plasticity, in terms of both regionalization and meristic change. The cervical spine gradually transformed in the evolutionary history of modern mammals from their non-mammlian therapsid ancestors (Fig. 2), a process which has been extensively described by Buchholtz et al. (2012).

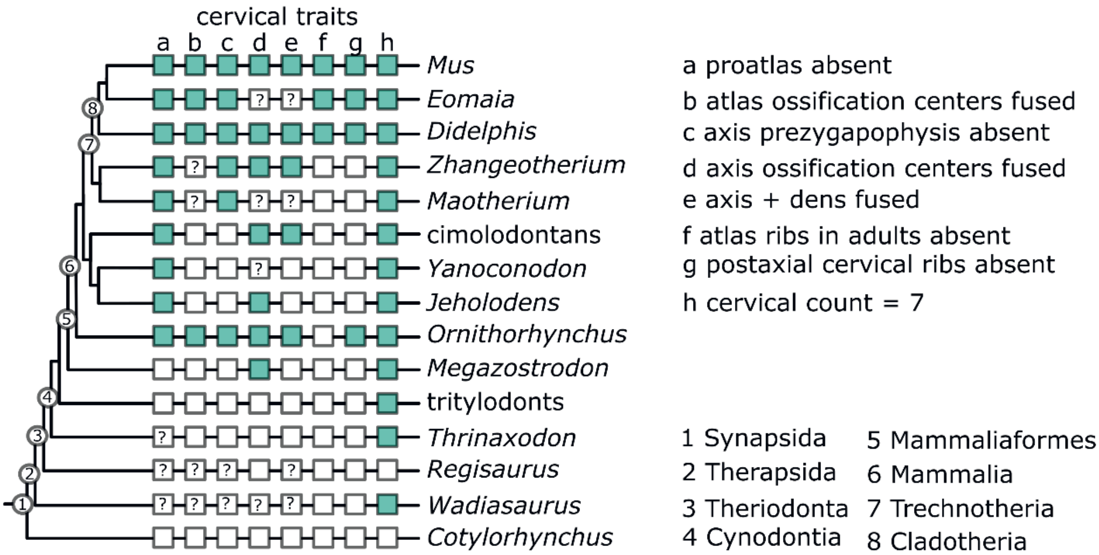

Figure 2 Trait evolution of the cervical spine across the synapsid-mammalian transition. Adopted and modified after Buchholtz et al. (2012). See references therein for character traits of the taxa.

However, a lot of homoplasy occurred during the evolution of the mammalian cervical spine, e. g., between australophenids (Monotremata and their stem group) and therians or between some haramiyidan allotherians and therians (Buchholtz et al. 2012; Bi et al. 2014). In short, three major trends can be traced by the fossil record: the fixation of the cervical count, the consolidation of the specialized cranio-cervical junction (atlas-axis complex), and the reduction and fusion of cervical ribs (Lessertisseur and Saban 1967; Buchholtz et al. 2012). According to the paleontological evidence (e.g., *Thrinaxodon*), the limitation to only seven cervical vertebrae dates back more than 200 million years into the Triassic (Jenkins 1971; Crompton and Jenkins 1973). However, the hypothesized developmental constraints in the evolution of mammalian cervical spine (Galis 1999; Narita and Kuratani 2005) most likely even characterized basal synapsids and thus significantly predated the origin of the Mammaliaformes and the mammalian crown group (Müller et al. 2010). The meristic limitation was followed by an early onset of the consolidation of the specialized head joint. The reptilian multiple elements occipitocervical complex was replaced by a two-element atlas-dens axis-joint due to the stepwise loss of the proatlas and axis' prezygapophyseal facets and the fusion of the different ossification centers of the atlas and axis, respectively (Jenkins 1969, 1971; Jenkins and Parrington 1976; Li and Luo 2006; Buchholtz et al. 2012; Chen 2015) (Fig. 2). Cervical rib modification, in contrast, was historically much more recent (Fig. 2), as movable postatlantal cervical ribs were still present in Cretaceous symmetrodonts (e.g., *Maotherium*, *Zhangheotherium*) (Li and Luo 2006; Luo et al. 2007; Buchholtz et al. 2012). In accordance, a modification of the cervico-thoracic junction due to the morphological specialization of the sixth cervical vertebrae (complete transformation of the fused rib rudiment into the ventral lamina or Chassaignac tubercle; Lessertisseur and Saban 1967) first occurred late in crown marsupials and placentals (Kielan-Jaworowska 1977a, b; Krause and Jenkins 1983). Generally, most derived cervical traits did not evolve until the rise of crown placentals, as even early eutherian mammals (e. g., zalambdalestids, asioryctitherians) retained several of the plesiomorphic features of monotremes and triconodonts (Kielan-Jaworowska 1977a, b, 1989). Overall, post-Triassic modification of the cervical spine in the lineage leading to modern mammals can be related to an increase in neck mobility in the sagittal plane, an elevated head/neck posture, and an increased neuromuscular control of the forelimb (Jenkins and Parrington 1976; Kielan-Jaworowska 1989). Most interestingly, the onset of the fixed cervical count was contemporaneous with the differentiation of the dorsal series into thoracic and lumbar spine and the inferred origin of the muscularized diaphragm, again highlighting the close interrelationship of locomotor-metabolic innovations and axial meristic constraints in mammalian evolution (Buchholtz et al. 2012; Buchholtz 2014; Galis et al. 2014).

Aims and concepts of the dissertation

This dissertation project was undertaken to improve the understanding of the evolutionary morphology of the mammalian neck. The head adopts a variety of postures during foraging, drinking, grooming, exploration, social interaction, and locomotion and the neck has to generate numerous head trajectories. This functional diversity of the neck as the main head actuator is contrasted by the limited number of cervical vertebrae that constitute the kinematic chain. As shown above, mammalian neck morphology is further canalized by multiple biomechanical determinants and deep-time conservatism. In-depth knowledge of the patterns of the disparity and constraints of the mammalian neck will enhance our understanding of the evolution of structures attributed to stay in evolutionary stasis.

This thesis is driven by three main research questions:
(i) What are the underlying patterns of neck disparity accounting for its functional diversity?
(ii) Do the developmental constraints and biomechanical determinants impact further morphological proporties (besides the number and shape of the cervial vertberae)?
(iii) What role do modularization and regionalization play in the evolutionary morphology of the mammalian neck?

Research in this specific field is generally focused on two aspects. First, evolutionary developmental studies have examined the patterns and processes resulting in the fixed number of seven cervical vertebrae across (almost) all mammals (Galis 1999; Narita and Kuratani 2005; Galis et al. 2006; Buchholtz et al. 2012; see also above). Second, several authors have analyzed the morphology of the cervical vertebrae and the shape trajectories descending down the cervical spine (i.e., from C1 to C7). They uncovered specific morphologies associated with each vertebral position within the neck skeleton, which are quite conserved across species and body size ranges (Krüger 1958; Johnson and O'Higgins 1996; Johnson et al. 1999; Breit and Künzel 2004; Buchholtz et al. 2012; Danowitz and Solounias 2015; Arnold et al. 2016; Randau et al. 2016; Randau et al. 2017). To extend the knowledge of the mammalian neck beyond the developmental 'bedrock' of meristic constrains and the shape differences among the vertebrae, this dissertation, on the one hand, aims to focus on so far unobserved aspects of neck morphology (i.e., allometry and musculoskeletal organization). On the other hand, findings from the different aspects (structure, development, function) are integrated in a synthetic approach and finally examined for general patterns governing neck disparity.

This thesis is cumulative. Accordingly, each of the following chapters (2 to 4) was written to stand on its own as independent publications. Each of them apply different approaches to the morphology of the neck accounting for the different aspects examined therein. However, some redundancy, for example in the introducing sections, is unavoidable. The individual manuscripts (Chapters 2 to 4) are followed by a synopsis to summarize the evidence gathered and to formulate the conclusions of the dissertation (Chapter 5).

Chapter 2 is an in-depth analysis of the allometry of the cervical spine across a large sample of mammalian species. The analysis is used to reveal what role body size and neck length play in neck disparity. Linear metrics of the cervical spine as a whole and of the individual cervical vertebrae as well as the vertebral proportions are analyzed with phylogentic comparatives methods.

In Chapter 3, both osteological and muscular topological data of the necks of 48 mammalian species are integrated within the same examination. The disparity of the necks' musculoskeletal organization is analyzed within the novel, state-of-the-art framework of anatomical network analysis. Neck organization and modularity are characterized by seven network parameters and interpreted in their morphological context. A disparity-through-time analysis allows for an evaluation of the evolution of neck organization before and after the Cretaceous–Tertiary boundary.

Chapter 4 combines findings from the development of the anterior-posterior Hox gene patterning of the neck in mammals and other amniotes with the shape differences of the vertebrae descending down the cervical spine. This approach aims to gain insights into the evolutionary morphology of the neck in extant tree sloths (*Bradypus* and *Choloepus*) as well as the conserved modularity of the mammalian neck in general. Modularity is discussed as a linkage of cervical development, vertebral shape, and neck function.

As obvious from research questions and manuscripts above, three basic concepts in evolutionary morphology are applied here to the mammalian neck: *constraints*, *disparity*, and *modularity*. As these terms, however, have different meanings and definitions for different researchers, they are briefly outlined and defined in order to clarify what is intended when they are used within the dissertation.

Evolutionary *constraints* can be described as limitations on the course or outcome of evolution that are caused by genetics, selection, function, or development (Maynard-Smith et al. 1985; Arnold 1992). The concept of constraints is often used with negative connotations in the sense of limitations on phenotypic variability, particularly regarding developmental constraints (Alberch 1982; Maynard-Smith et al. 1985). In contrast, the concept of constraints is here used as directing causes of evolutionary change (Gould 2002). In this positive connotation, constraints act to urge or promote change in a particular evolutionary direction (Gould 2002). However, it is not used here in its loosest definition, i.e. that everything is possible if there is enough time or when favoring circumstances arise ('evolutionary habits'; see Scholtz 2010). In contrast, the historical (developmental, phylogenetic), structural, and functional constraints define the edges of the evolutionary solution field of a particular structure (Seilacher 1970; Reif et al. 1985; Seilacher and Gishlick 2014). In this conceptional use, even drastic variation is not 'forbidden' and natural selection is not prevented from acting (Gould 2002). The evolutionary trace of a structure, however, is 'channeled' and thus might not ultimately result in the 'best adapted' solution (Gould and Lewontin 1979; Gould 2002).

Disparity is here defined as morphological diversity or that diverse forms of a certain structure have evolved (Foote 1997). It is distinguished from the pure term of 'diversity', as it implies high species number and specifications rates. Indeed, species diversity is no necessarily coupled with disparity (Foote 1993, 1997; Adams et al. 2009; Minelli 2015). Disparity thus correlates more closely with the number of higher taxa than with the number of species (Gould 1989). Today, the concept of disparity is usually used in the context of the numerous quantitative measurement approaches that have been developed in the last decades (Foote 1997; Erwin 2007). However, disparity is here used in its basic meaning of the diversity of morphological forms unless quantitative methods are directly described in the chapters.

The concept of evolutionary *modularity* corresponds to the recognition that the phenotype can be decomposed into parts. Modules are tightly integrated by numerous and usually strong internal interactions compared to the few and weak interactions that connect different modules (Klingenberg 2008). The internal interactions, however, occur in different contexts and on different level of integration, like genetics (e. g., pleiotropy), development, anatomical organization, or function, and thus result in different types of modules (i.e., genetic modules, developmental modules etc.; Olson and Miller 1999; Eble 2005; Wagner et al. 2007; Klingenberg 2008; Esteve-Altava 2017). The interplay and relationship of the different types of modules and the structured associations between the evolutionary divergence in different traits finally result in evolutionary modules and modularity (Goswami 2006; Klingenberg 2008; Goswami et al. 2014). In terms of the vertebrate axial skeleton (vertebral column), modularity is usually referred as ‘regionalization’ based on the chain-like organization of serial elements (e. g., Cohn and Tickle 1999; Polly et al. 2001; Ahlberg et al. 2005; Narita and Kuratani 2005; Wellik 2007; Mallo et al. 2010; Müller et al. 2010; Ward and Mehta 2014; Randau et al. 2017). Both terms are used synonymously here for the neck skeleton/cervical region of mammals, implying a potential decomposition on different levels of integration (structural/organizational, developmental, functional).

Overview of Manuscripts

Chapter 2

Arnold P, Amson E, Fischer MS. Differential scaling patterns of vertebrae and the evolution of neck length in mammals.

Published in *Evolution,* 2017, 71(6), 1587–1599.

PA designed the study, visited all museum collections, collected all data, conducted the analyses, wrote the R script for the ternary analysis, interpreted the results, prepared all figures and the supplementary material, and wrote the manuscript. EA wrote the R script for the phylogenetic comparative methods, constructed the phylogenetic time tree, and contributed to the discussion of the results. Martin S. Fischer provided conceptual help and contributed to the discussion of the results.

Chapter 3

Arnold P, Esteve-Altava B, Fischer MS. Musculoskeletal networks reveal topological disparity in mammalian neck evolution.

In review, submitted to *BMC Evolutionary Biology*

Reviews received on 7.7.2017, revised manuscript resubmitted on 5.8.2017

PA designed the study, collected all data, prepared adjacency matrices, constructed the phylogenetic time tree, wrote the R script for the relative variability and disparity-through-time analysis, interpreted the results, prepared all figures and the supplementary material, and wrote the manuscript. PA and BEA conducted the phylogenetic analyses. BEA wrote the R script for the network parameter and modularity analyses and contributed to the discussion of the results. MSF provided conceptual help and contributed to the discussion.

Chapter 4

Böhmer C, Amson E, **Arnold P**, van Heteren AH, Nyakatura JA. Mammalian Hox code and morphological modularity: homeotic transformations explain departure from the mammalian 'rule of seven' in sloths.

Submitted to *Proceedings of the National Academy of Science* on 20.8.2017

CB and JAN designed the study. CB did the analysis, interpreted the data and drafted the manuscript. EA, PA and AHvH collected the data. CB, PA and JAN prepared the figures. All authors contributed to the discussion and the final manuscript version.

I have read the authors' contributions stated above and confirm their correctness.

Prof. Dr. Martin S. Fischer (supervisor)

Chapter 2

Differential scaling patterns of vertebrae and the evolution of neck length in mammals

published in *Evolution* as:
Arnold P, Amson E, Fischer MS (2017). Differential scaling patterns of vertebrae and the evolution of neck length in mammals. *Evolution*. 71(6), 1587–1599

In mammals, the structural requirements associated with evolutionary modifications of neck length have to be met with a fixed number of vertebrae. It has not been clear whether body size influences the overall length of the cervical spine and its inner organization (i.e., if the mammalian neck is subject to allometry). Our results indicate that the main source of variation in the mammalian neck stems from the disparity of overall cervical spine length. The mammalian neck reveals how evolutionary disparity manifests itself in a structure that is otherwise highly restricted by meristic constraints.

PA designed the study, visited all museum collections, collected all data, conducted the analyses, wrote the R script for the ternary analysis, interpreted the results, prepared all figures and the supplementary material, and wrote the manuscript. EA wrote the R script for the phylogenetic comparative methods, constructed the phylogenetic time tree, and contributed to the discussion of the results. Martin S. Fischer provided conceptual help and contributed to the discussion of the results.

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Differential scaling patterns of vertebrae and the evolution of neck length in mammals

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Almost all mammals have seven vertebrae in their cervical spines. This consistency represents one of the most prominent examples of morphological stasis in vertebrae evolution. Hence, the requirements associated with evolutionary modifications of neck length have to be met with a fixed number of vertebrae. It has not been clear whether body size influences the overall length of the cervical spine and its inner organization (i.e., if the mammalian neck is subject to allometry). Here, we provide the first large-scale analysis of the scaling patterns of the cervical spine and its constituting cervical vertebrae. Our findings reveal that the opposite allometric scaling of C1 and C2–C7 accommodate the increase of neck bending moment with body size. The internal organization of the neck skeleton exhibits surprisingly uniformity in the vast majority of mammals. Deviations from this general pattern only occur under extreme loading regimes associated with particular functional and allometric demands. Our results indicate that the main source of variation in the mammalian neck stems from the disparity of overall cervical spine length. The mammalian neck reveals how evolutionary disparity manifests itself in a structure that is otherwise highly restricted by meristic constraints.

KEY WORDS: Allometry, mammalian cervical spine, neck evolution, proportions.

Adaptive evolutionary acquisitions involve the generation of variation and subsequent natural selection. Some structures, however, seem to resist evolutionary change and remain in a morphological stasis (e.g., Eldredge and Gould 1972; Smith et al. 1985; Sturmbauer and Meyer 1992; Suno-Uchi et al. 1997; Galis and Metz 2003; Witt et al. 2003; Lecompte et al. 2005; Narita and Kuratani 2005; Hughes 2007; Lavoué et al. 2011). One of the most prominent examples of morphological stasis in vertebrates is the mammalian cervical spine as seven cervical vertebrae are consistently found across almost all mammals (Galis 1999; Narita and Kuratani 2005). According to the paleontological evidence, this consistency dates back more than 200 million years (Jenkins 1971; Crompton and Jenkins 1973). It contrasts with the high variation in the number of neck vertebrae found across other extant and extinct tetrapod lineages (Müller et al. 2010). For example, evolutionary variation in avian neck length occurs locally by the addition of cervical vertebrae (Van Der Leeuw 1991; Van Der Leeuw et al. 2001). In birds, there seem to be no developmental constraints that fix their number (i.e., variation in vertebral number is rarely accompanied by malformation or cancer) (Fox 1912; Effron et al. 1977; Adelman et al. 1988; Barja et al. 1994; Perez-Campo et al. 1998; Galis 1999).

The developmental framework of the mammalian cervical spine has gained considerable attention in the last few decades. Several studies have revealed processes in the prenatal development constraining meristic variability in the neck (Galis 1999;

Galis and Metz 2003; Galis et al. 2006; Galis and Metz 2007; Buchholtz 2012; Buchholtz et al. 2012; Hirasawa and Kuratani 2013; Buchholtz 2014; Hirasawa et al. 2016). These findings give the rationale for the evolutionary stasis in the number of neck vertebrae across mammals. In some mammalian clades, however, natural selection favored the increase or the decrease in neck length, such as in giraffes and whales, respectively. The requirements associated with these neck length modifications have to be met within the fixed number of cervical vertebrae (Woltering and Duboule 2015). The pattern of vertebral size modification is hence of particular importance, as the general shape of the individual vertebrae (C1–C7) is quite conserved across mammalian lineages and their body size range (Johnson and O'Higgins 1996; Johnson et al. 1999; Buchholtz and Stepien 2009; Buchholtz et al. 2012; Buchholtz et al. 2014; Arnold et al. 2016). Nevertheless, it is not clear whether scaling of neck length is achieved by uniform modification of the whole cervical spine or by individual vertebra length alteration. Furthermore, it is not clear whether the overall length of the cervical spine and its inner organization are influenced by body size (i.e., subject to allometry).

Although altering body size is a crucial component of mammalian evolutionary diversification, the associated biomechanical implications raise an important evolutionary challenge (Thompson 1917; Huxley 1932). Scaling analyses of vertebral metrics among particular mammalian clades have recently provided crucial insights into the evolutionary variation of the axial skeleton (Viglino et al. 2014; Jones 2015; Jones and Pierce 2016; Randau et al. 2016). It is worth noting, however, that most investigations of cervical variation to date have focused on particular clades with either an aberrant number of vertebrae (i.e., departing from the seven-vertebrae rule, namely sloths and the manatee) (Buchholtz et al. 2007; Buchholtz and Stepien 2009; Hautier et al. 2010; Varela-Lasheras et al. 2011; Endo et al. 2013; Buchholtz et al. 2014) or with an extreme neck length (Lankester 1908; Solounias 1999; Van Schalkwyk et al. 2004; Badlangana et al. 2009; Van Sittert et al. 2010; Mitchell et al. 2013; Danowitz and Solounias 2015; Danowitz et al. 2015; Gunji and Endo 2016). Naturally, these approaches do not encompass the full range of mammalian cervical length and body size. Krüger (1958) compared the anatomy of the cervical vertebrae of most mammalian orders but did not use a quantitative approach. Accordingly, to date no large-scale comparative dataset exists that would permit the inference of general patterns of cervical scaling to body size or to neck length.

The scope of our study is (1) to infer the relationship between cervical spine length and body size across the full range of mammalian sizes; (2) to examine patterns of cervical spine length and individual vertebral length scaling in mammals in general, as well as in several subclades; (3) to assess whether scaling is uniform among individual vertebrae; and (4) to establish a general rule that governs neck design in mammals. We compare the lengths, proportions, and scaling properties of the individual cervical vertebrae as well as the whole cervical spine across a large dataset of mammals. The final goal of our study is to look for similarities in cervical spine construction across mammals. We want to confront our findings with the neck's biomechanical determinants in mammalian evolution. We also aim to discuss them in the context of the fixed number of seven vertebrae found in virtually all mammals.

Mechanical models suggest that the vertebral centra (the body of the vertebra) form the major compressive support structure in the neck region (Slijper 1942; Kummer 1959a,b; Smit 2002). Thus, we focused on the scaling patterns of the vertebral centra. They most directly relate to variation in compressive loadings, which reflects the disparity in body size, head size, and neck length.

Material and Methods

DATA ACQUISITION

Our sample consists of 467 specimens representing 352 species of mammals. All main clades of monotremes, marsupials, and placentals were represented (Fig. 1; for more details, see Table S1). The sample comprises of mammals that employ various foraging strategies (e.g., carnivores, herbivores, omnivores) and locomotor specializations (e.g., terrestrial, fossorial, aquatic, saltatorial, biped, volant). Taxa with an aberrant number of cervical vertebrae (i.e., sloths and manatees) were excluded from the analysis. Taxa in which some of the vertebrae are fused were only included if the borders of subsequent vertebral bodies were clearly recognizable (e.g., in cetaceans and some xenarthrans). The sampled specimens are housed in the collections of the Phyletisches Museum Jena, Senckenberg Forschungsinstitut und Naturkundemuseum Frankfurt, Museum für Naturkunde—Leibniz-Institut für Evolutions— und Biodiversitätsforschung zu Berlin, Staatliche Museum für Naturkunde Stuttgart and Naturkundemuseum Erfurt. CT scans from German zoo animals provided by the Hospital of Small Animal Surgery, University of Gießen, were also included in the dataset (see Table S2 for a complete list of specimens). For species represented by more than one specimen, mean values were used in all subsequent calculations.

Individual cervical vertebra lengths were measured along the ventral side of the vertebral bodies in the sagittal plane (i.e., vertebral centrum length) using a digital caliper (accuracy: 0.01 mm). Atlas length was measured as the length of the ventral half of the bony ring (i.e., its thickness in a craniocaudal direction) excluding the caudally directed ventral tubercle. The odontoid process was excluded from the measurement of axis length, as it does not contribute to cervical spine length due to its position within the bony ring of the atlas when articulated. For specimens with

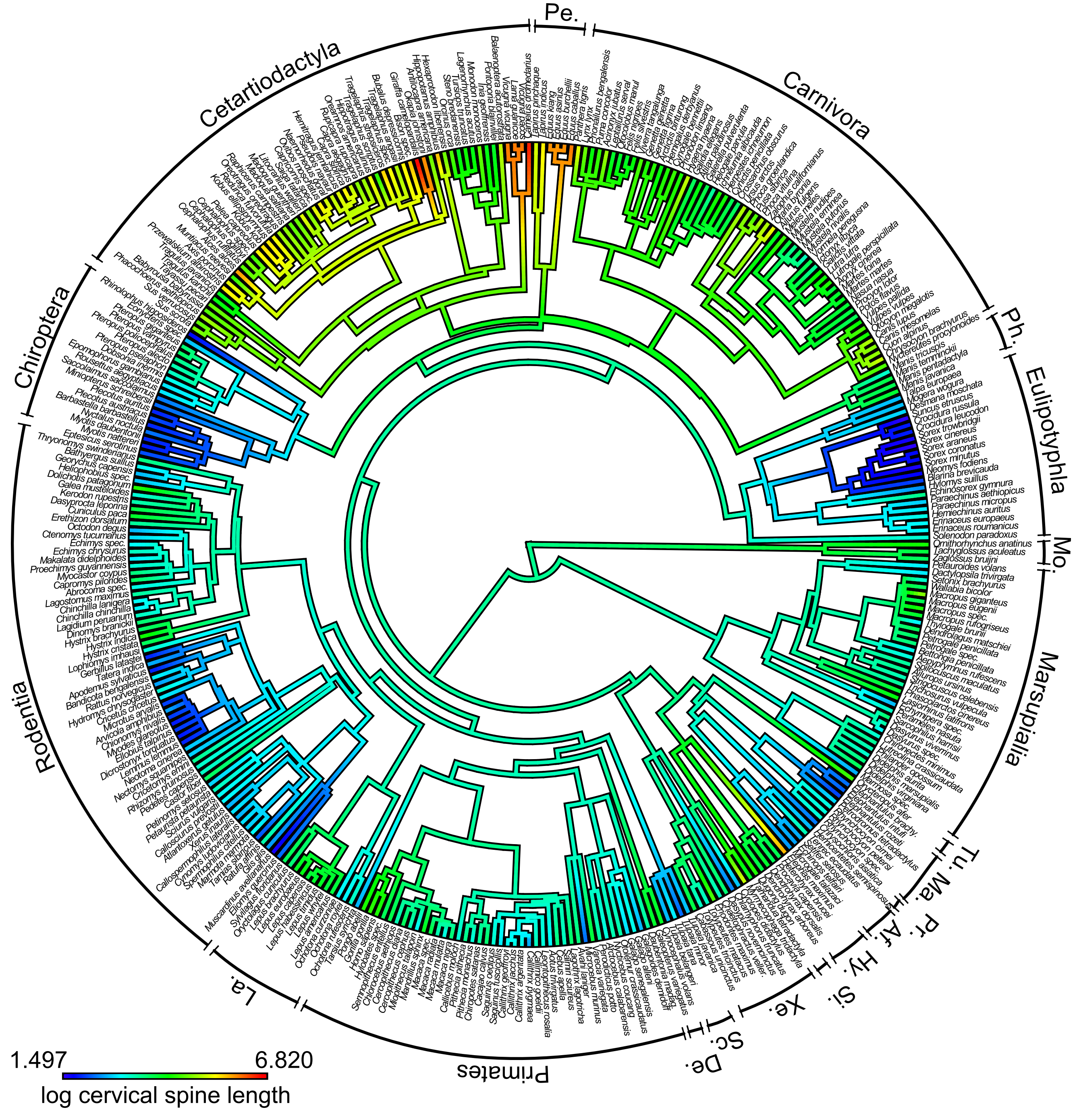

Figure 1. **Timetree of the 352 mammalian species from 272 genera sampled for this study. The cervical spine length (log-transformed) is mapped on the branches. Af., Afrosoricida; De., Dermoptera; Hy., Hyracoidea; La., Lagomorpha; Ma., Macroscelidea; Mo., Monotremata; Pe., Perissodactyla; Ph., Pholidota; Pr., Proboscidea; Sc., Scandentia; Si., Sirenia; Tu., Tubulidentata; Xe., Xenarthra.**

vertebrae smaller than 3 mm, cervical spines were scanned at a voxel size of 37 μm at the Institute of Diagnostic and Interventional Radiology, Jena University Hospital. Vertebral lengths were measured subsequently from extracted surfaces in the software Amira 5.4.2 (Visage Imaging, Richmond, Australia). Total cervical spine length was calculated as the sum of the seven vertebrae and did not include any estimates of the size of the intervertebral discs or intercentrum cartilage (see Badlangana et al. 2009). Vertebral proportions were calculated as the percentage of the total cervical spine length represented by each vertebra.

Body mass was used as a body size proxy. For the majority of collection specimens, the body mass was not available. The majority of information was hence taken from the AnAge database (Human Aging Genomic Resources, University of Liverpool, Liverpool, United Kingdom) (Tacutu et al. 2012) (accessed at: http://genomics. senescence.info/species/) and completed from the literature (Nowak 1999; Kingdon 2015). Additionally, we also used tibial length as an alternative body size proxy (see Schmidt and Fischer 2009), which is individually associated with the sampled specimens. See Table S3 for the original data.

STATISTICS

The overall cervical spine length and individual vertebral lengths were investigated to test whether allometric scaling is a significant source of their variation. Accordingly, they were regressed against a body size proxy to assess their relationship to body size for all mammals. All regressions were additionally performed for Carnivora, Cetartiodactyla, Marsupialia, Primates, and Rodentia (>70% of the total sample) to compare deviations from the general mammalian pattern. These regressions were also performed on (super)familial taxonomic levels (Bovidae, Caviomorpha, Cercopithecidae, Felidae, Leporidae, Macropodidae + Potoroidae, Muroidea, Mustelidae, Platyrrhini, Pteropodidae, Sciuromorpha, Soricidae) in which at least nine species were available.

R 3.3.1 (R Core Team 2016) was used for all calculations with the following significance levels of P values: $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$ (R script provided in the supplement). All data were right-skewed and highly kurtotic (skewness >> 0***, D'Agostino test; (D'Agostino 1970); kurtosis >> 3***, Anscombe–Glynn test (Anscombe and Glynn 1983); "moments" package; (Komsta and Novomestky 2014). To account for this, they were log-transformed.

Phylogenetically informed methods were used to take the phylogenetic relationships of the sample taxa into account. The Timetree of life (TOL; Hedges et al. 2015) resolved at the species level (accessed at http://timetreebeta.igem.temple.edu/) was modified according to our sampling with Mesquite 3.10 (Maddison and Maddison 2011). See additional details on the timetree construction in the supplements; the resulting timetree is given as a nexus file. Following the recommendation of Revell (2010), we used the generalized least squares function of the "nlme" 3.1-128 package (Pinheiro et al. 2008), with Pagel's λ (Pagel 1999) correlation structure ("ape" 3.5 package (Paradis et al. 2004). This method simultaneously estimates the regression model and phylogenetic signal (using Pagel's λ, which outperforms other commonly used indices (Münkemüller et al. 2012). For some of the subclades with small sample sizes, the phylogenetic signal was so small that the regression model was not successfully estimated. In these cases, we used traditional generalized least-square regressions. A slope test was used to compare the scaling of each relationship to the coefficient denoting isometry (with body mass: 1/3; with tibial length: 1), using the Student's t distribution ("pt" function). A correction for multiple testing (Holm–Bonferroni method, "p.adjust" function) was finally applied to the slope test P values.

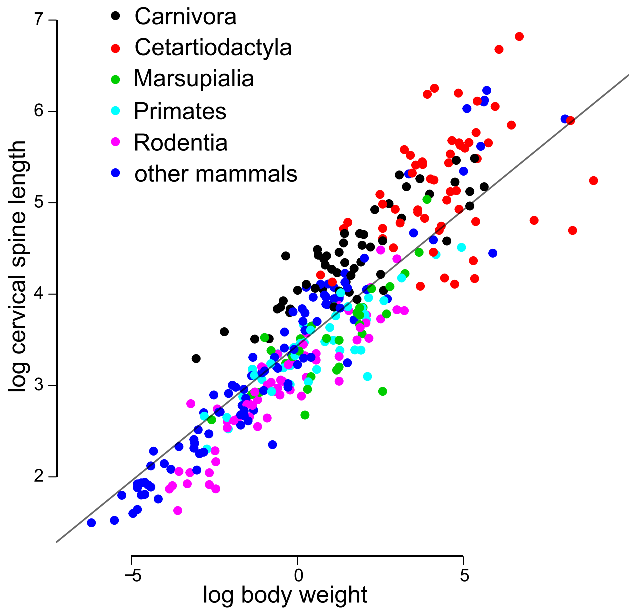

Figure 2. Regression of log cervical spine length against log body weight for 352 mammalian species. Colors code for the major mammalian clades. The gray line represents the phylogenetic informed regression for all mammals.

We also used a phylogenetically informed multivariate approach to investigate the relationships among the vertebral lengths, the cervical spine length, and body weight, thanks to the "phyl.pca" function of the "phytools" 0.5-38 package (Revell 2012). Additionally, patterns of variation according to cervical organization were further explored and visualized using a ternary plot ("ggtern" 2.2.0 package; (Hamilton 2016) and 95% confidence lines (using Mahalanobis distances) on groups of covarying vertebrae (inferred from the PCA, see below).

Results

SCALING OF OVERALL CERVICAL SPINE LENGTH

The overall cervical spine length scales with negative allometry against body weight (Figs. 2 and 3; Table S4) across all mammals (slope = 0.3**) as well as in the individual analyses of carnivorans, cetartiodactyls, marsupials, primates, and rodents (slope = 0.25–0.28; the deviation from isometry, however, is not significant in the latter three). Thus, the cervical spine shortens relatively as body size increases. This result reveals the importance of taking phylogeny into account, as a traditional linear regression finds positive allometry in the same data. The residuals from the regression (scatter around the regression line) are

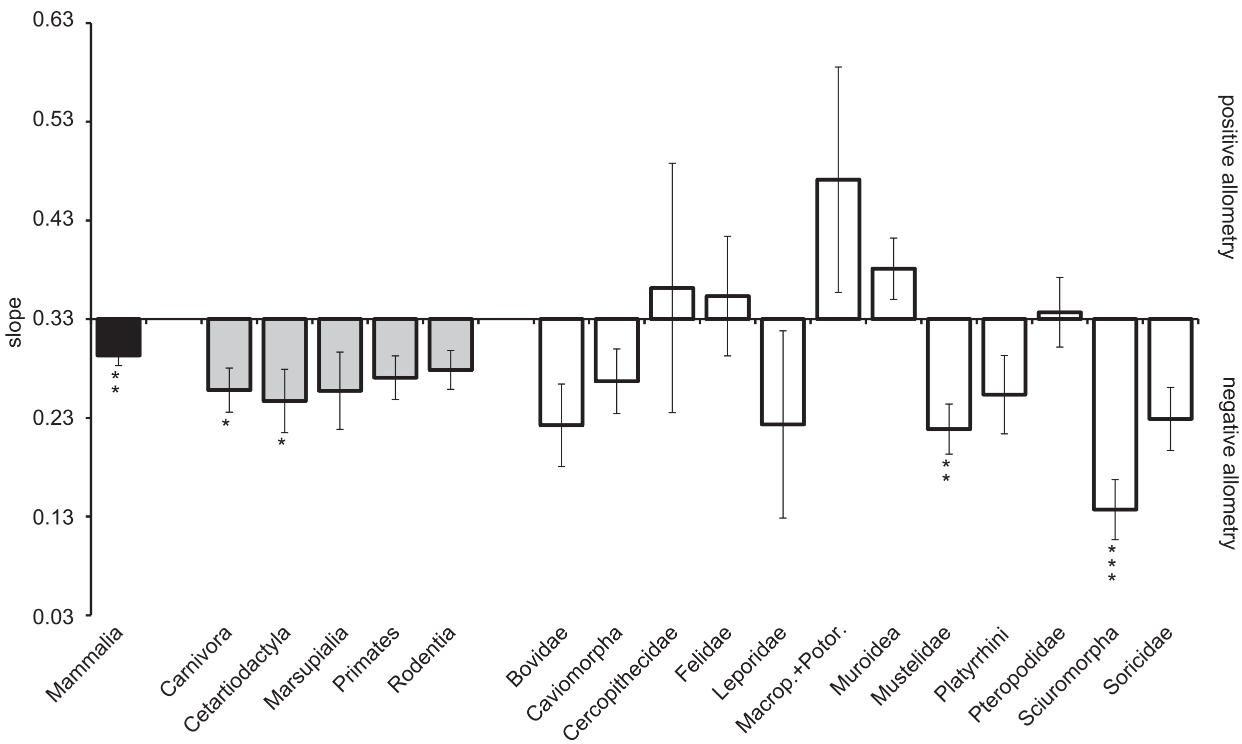

Figure 3. **Comparison of the slopes for the regressions of log cervical spine length against log body weight for mammals in general (dark gray), the major mammalian clades (light gray), and on the (super)familial level (white). The error bars represent the SE of the slopes. Asterisks indicate the significance of slope tests for allometry (i.e., significant different from isometry, corrected for multiple testing, significance levels: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).**

large, specifically in carnivorans, cetartiodactyls, and marsupials, and especially for large-sized species (Fig. 2). Similar results are also found when looking at the (super)familial taxonomic level, however, with much more variability (Fig. 3). At this level, the cervical spine also scales either isometrically or with negative allometry depending on the groups. The macropodid–potoroid clade (and to a lesser extent the muroids) is the only exception as it scales with positive allometry. Regressions on tibial length (the alternative body size proxy) revealed very similar results (Table S5).

SCALING OF THE INDIVIDUAL CERVICAL VERTEBRAE

In mammals in general, all individual cervical vertebrae apart from C1 scale with negative allometry and thus relatively shorten with increasing body size (Fig. 4; Table S6). C1, in contrast, scales with positive allometry. These slope differences result in a cervical length internal organization (i.e., the set of individual vertebra proportions) that changes with varying body size. Similar patterns are again found in carnivorans, cetartiodactyls, marsupials, primates, and rodents, particularly for C2–C7 (Fig. 4 and Table S5). In marsupials, however, C1 scales with strong negative allometry.

Significance at the (super)familial level is low due to reduced sample sizes. However, in most cases, C2–C7 describe patterns similar to those of the larger clades (Table S6). C1 scales with positive allometry in taxa, which include a wide range of body sizes (e.g., bovids, felids). In contrast, it scales with negative allometry or isometry in taxa in which differences in body size are low (e.g., sciuromorphs, soricids). Regressions on tibial length revealed very similar results (Table S5).

PHYLOGENETIC PRINCIPLE COMPONENT ANALYSIS AND VERTEBRAL COVARIATION

In addition to the bivariate regression analyses, we also conducted a phylogenetic PCA to reveal more detailed patterns of vertebral covariation (Fig. 5). PC1 and PC2 together account for more than 96% of total variation (Table S7). PC1 loadings are high for all parameters (Table S7). PC1 therefore does not elucidate any further conclusions regarding particular vertebral patterns. However, when examining PC1 against PC2, the loading vectors form three distinct groups. The C1 vector is widely separated from the other vertebrae vectors and plots close to the body weight vector. The second group is composed of C2, C7 (i.e., the vertebrae making transition with the rest of the spine), and the whole cervical spine length vectors. The third group includes the

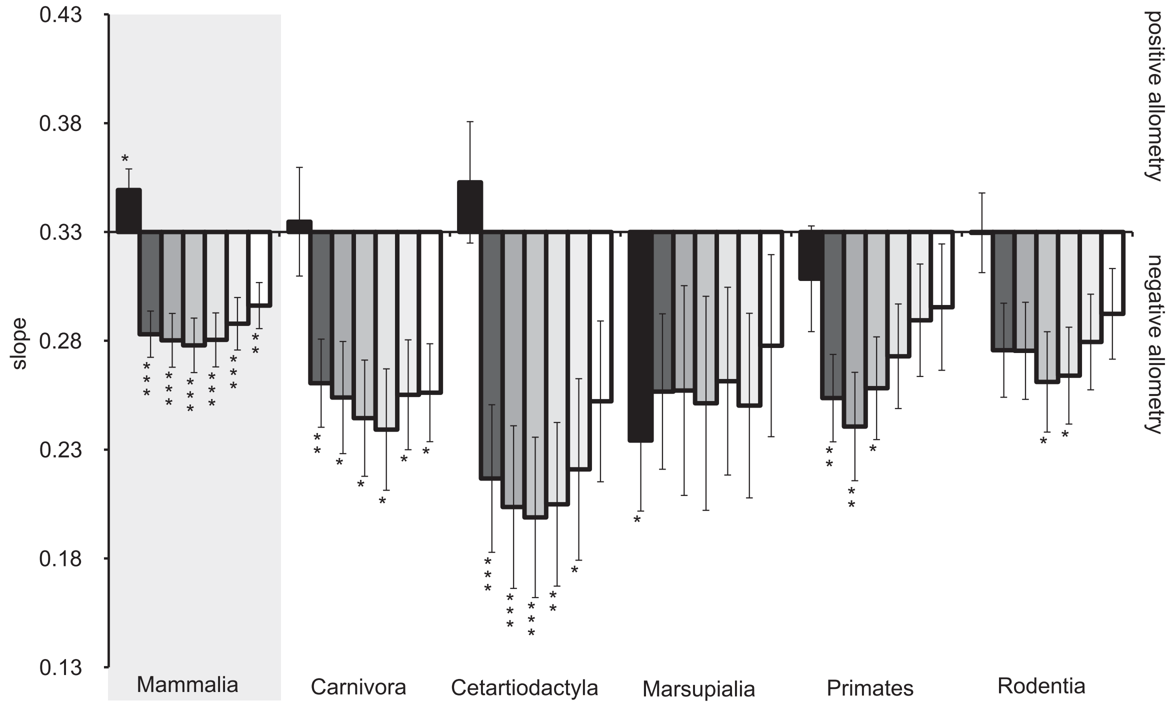

Figure 4. Comparison of the slopes for the regressions of log vertebral lengths against log body weight for C1 (dark gray) to C7 (white) in mammals in general and the major mammalian clades. The error bars represent the SE of the slopes. Asterisks indicate the significance of slope tests for allometry (i.e., significant different from isometry, corrected for multiple testing, significance levels: *P < 0.05; **P < 0.01; ***P < 0.001).

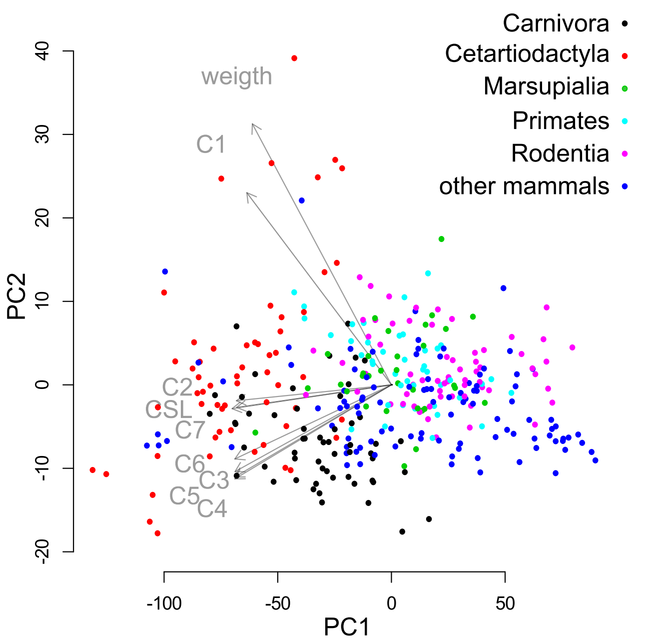

Figure 5. Results of the phylogenetic principle component analysis (phylPCA) on body weight, cervical spine length (CSL), and vertebral lengths (C1–C7). PC1 and PC2 together account for more than 96% of total variation. Colors code for the major mammalian clades. The loading vectors (gray arrows) form three distinct groups: C1 + body weight; C2 + C7 + CSL; C3–C6.

vectors of C3–C6 (i.e., the mid-cervical vertebrae), which strongly covary.

VERTEBRAL PROPORTIONS

The proportions of the three classes of cervical vertebrae suggested by the loading vectors of the phylogenetic PCA (i.e., C1, C2 + 7, and C3–C6) are visualized using a ternary graph (Fig. 6). Most species are densely clustered in a small portion of the ternary space (framed by the triangular 95% confidence line). This indicates that the three-class pattern of cervical organization is quite uniform across most mammals. However, there are three main deviations from this pattern that can be linked to particular functional demands (Figs. 6 and 7). First, long-necked mammals including the giraffe (*Giraffa camelopardalis*), camelids, and small-horned/nonhorned antilopin bovids cluster on the bottom right. They possess relatively long C3–C6 but short C1 and C2 + 7 (especially C7; Fig. 7). Second, several (but not all) fossorial species cluster on the top. These species have relatively long C2 + 7 but short C1 and C3–C6 (e.g., the marmot [*Marmota marmota*], the cape golden mole [*Chrysochloris asiatica*], and several dasypodid armadillos). And third, located in the bottom left are the large-headed and/or fully aquatic species possessing a massive C1 but relatively short C3–C6 (cetaceans, the elephant [*Elephas maximus*], the dugong [*Dugong dugon*], and large bovids).

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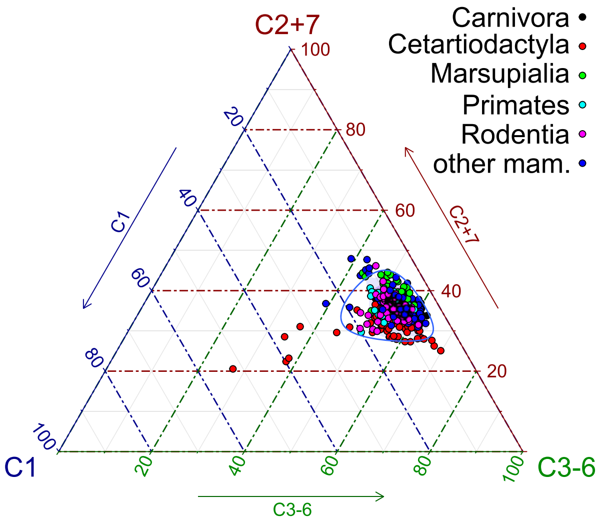

Figure 6. **Ternary plot visualizing the proportions of the three vertebral classes (C1; C2 + C7; C3–C6) for the necks of 352 mammalian species. Colors code for the major mammalian clades. The majority of mammals densely clusters in only a small fracture of the full ternary space (framed by the blue 95% confidence line) suggesting an only limited variation in vertebral proportions. Only few species deviate from this pattern in three directions (shaded in gray; see Fig. 7).**

The ternary plot also reveals the diversity of cervical spine traits among cetartiodactyls (red dots in Fig. 6). They occupy a large but continuous range in the ternary space. They range from large-headed but short-necked species (cetaceans, hippopotamids, large bovids) at the bottom right to medium-length necked species in the center (suids, tayassuids smaller sized pecorans) up to slender-headed but long-necked species on the bottom right (cervids, antilopines, giraffids, camelids).

Discussion

BODY SIZE AND NECK LENGTH IN MAMMALS

The general mammalian trend for the overall cervical spine length is to decrease with increasing body size. This was expected because the weight of the head increases (e.g., Cardini and Polly 2013; Cardini et al. 2015) with a power of three, whereas the stress-resisting cross-sectional area of the neck only increases with a power of two (Preuschoft and Klein 2013). To reduce neck bending moment, a relative decrease in the distance between the head's center of mass and its center of rotation (i.e., the cervico-thoracic junction) is required. This results in the negative allometry observed in the neck length scaling. This interspecific structural allometry (changes in bone structure with increasing body size) (McMahon 1973; McMahon 1975; Alexander et al. 1979) provides an important solution to maintaining acceptable safety factors in the neck skeleton (particularly in large mammals). A stouter cervical spine can withstand greater peak stresses (Alexander et al. 1979; Jones 2015). Negative allometry in the length of the cervical spine matches the results from the lumbar spine (e.g., Halpert et al. 1987; Majoral et al. 1997; Jones 2015). This suggests common body size constraints on the axial regions due to the combined function of load bearing and motion. In the mammalian clades in which cervical spine length scales isometrically (predominantly those of lower body sizes), postural allometry (changes in posture with increasing body size) (Alexander 1981; Bertram and Biewener 1990; Christiansen 1999; Biewener 2000) might also play an important role in reducing peak stresses and neck bending moment. For instance, small quadrupedal mammals raise their neck in a nearly vertical position and thereby reduce the lever arm of the head weight (especially during resting) (Vidal et al. 1986; Graf et al. 1995b).

The scatter around the regression line (Fig. 2) shows that cervical spine scaling is not uniform across mammalian lineages and that a good approximation of actual neck length cannot be extrapolated from body size in all clades (particularly for large-sized species and in carnivorans, cetartiodactyles, and marsupials). This variability is most likely due to the diversity of functional demands on the neck, as it is the main head actuator during daily activities (grooming, mating, drinking, exploration/sensing, and different modes of locomotion, posture, and foraging) (Heidweiller et al. 1992).

Departing from the uncovered overall allometric scaling, we observed that the cervical spine has been elongated beyond biomechanical predictions in some lineages. This is permitted by the extension of passive bracing elements. Camelids, giraffids, equids, and some antilopin bovids are characterized by a well-developed nuchal ligament permitting the stabilization of a long neck (Mobarak and Fouad 1977; Dimery et al. 1985; Bianchi 1988; Endo et al. 1997; Gellman and Bertram 2002; Preuschoft and Klein 2013). It is often associated with a coelongation of the limbs (Simmons and Altwegg 2010), which increases cursoriality while allowing the head to reach the ground. In contrast to other clades, the kangaroo *sensu lato* (macropodid-potoroid clade) show a strong positive allometry of the cervical spine. This is most likely related to their upright posture and bipedal–saltatorial locomotion (e.g., Grand 1990; Bennett and Taylor 1995; Chen et al. 2005). As the head is balanced on top of a vertical cervical column, negative allometry to reduce neck bending moment is not required. It is noteworthy that the relatively long neck of the kangaroo is regarded as providing increased head mobility to compensate for the increasing rigidity of the rest of the axial skeleton with increasing body size (Chen et al. 2005).

INTERNAL ORGANIZATION OF THE CERVICAL SPINE

The atlas (C1) is characterized by a unique scaling pattern, being the only vertebra that scales with positive allometry across

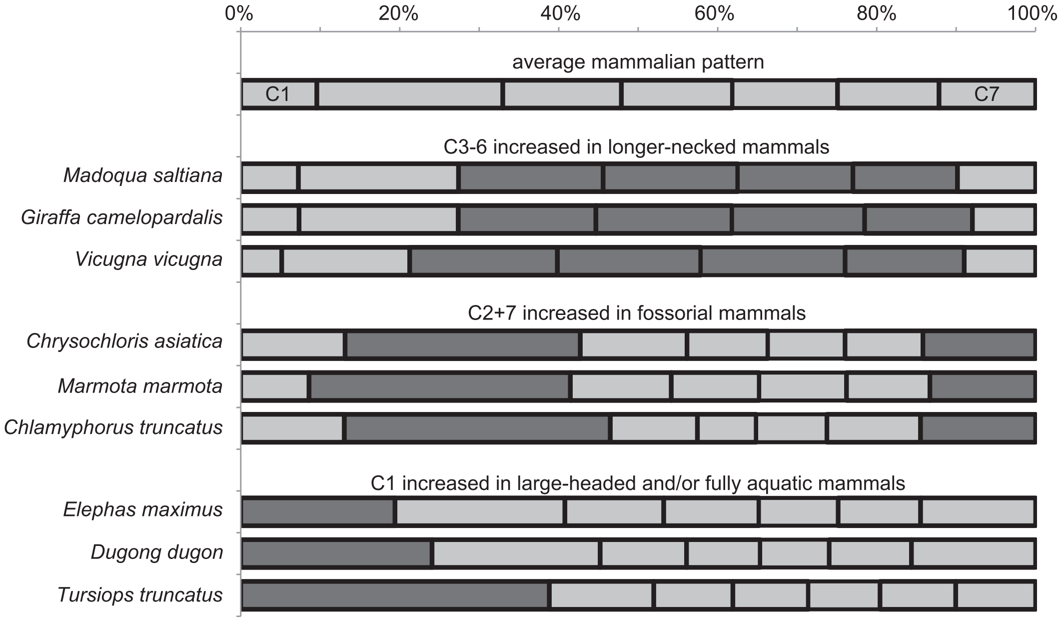

Figure 7. **Average internal organization of the mammalian neck compared to species representing the extremes of vertebral variation under altered loading regimes. The bars represent the vertebral proportions of C1–C7 (from left to right). Dark gray areas indicate those vertebra whose proportion are increased.**

all mammals. C2–C7 scale with negative allometry and are thus responsible for the overall reduction of the cervical spine length with increasing size. Among most mammals, the cervical internal organization is quite uniform and C1 accounts for most of the observed variation. The allometric pattern of C1 and the variability of its relative length reflect mammalian skull diversity in terms of size, weight, and posture (e.g., Manfreda et al. 2006). The atlas transfers the load of the head to the rest of the cervical spine. It provides not only the articular facets for the occipital condyles (which also increase with body size), but also the area of origin of the important monoarticular suboccipital muscles. Thus, despite the need for reducing neck length with increasing body size, the increase in C1 length maintains the stability of the craniocervical junction with increasing head size. Despite the close functional and developmental integration of C1 and C2 (Evans 1939; Jenkins 1969), their scaling within the cervical spine is completely different.

The phylogenetically informed PCA revealed important patterns in the construction of the cervical spine. Three vertebral classes were recognized: C1, C2 + C7, and C3–C6 (Fig. 5). They, respectively, correspond to three functional regimes: the accommodation of the head, the transition with the rest of the spine, and the inner bulk of the neck. When considering these three classes, it is most noteworthy that the internal organization of the cervical spine is found as particularly uniform across mammals (Fig. 6). Both the scaling patterns of the individual vertebrae and their complex interrelationship represent a general principle that governs neck design in mammals.

This pattern can nevertheless be drastically changed in species with extreme loading regimes. Camelids, giraffids, and some antilopin bovids, which include the species with the longest necks in our dataset, all have very similar proportions, including very long C3–C6 (65–70%) but short C1 and C2 + 7, especially C7 (Fig. 7). In these species, skulls are long but relatively slender, involving a reduced load bearing function for C1. Their general neck posture has to become steeper to bring the center of mass of the head closer to the center of rotation of the neck, that is, the cervicothoracic junction (thus reducing neck bending moment). This is enabled by a shortening of C7 as shorter vertebrae decrease the radius of curvature of the concerned articulation (Preuschoft and Klein 2013). Similar cervical traits are also found in extinct long-necked mammals, such as the "South American native ungulate" *Macrauchenia* (Litopterna, Macraucheniidae) (Huxley 1861; Cope 1891) or the giant rhinoceros *Paraceratherium* (Perissodactyla, Hyracodontidae) (Forster-Cooper 1911; Osborn and Berkey 1923; Granger and Gregory 1936). In contrast, some fossorial species have relatively long and massive C2, resulting in C1 and C2 together representing more than 40% of the total cervical spine length (Fig. 7). As a result, the cranial region of the neck is stabilized, and the head fulcrum is enhanced but overall neck mobility is reduced (Bogduk and Mercer 2000). This is further enhanced in some lineages with the fusion of C2 with midcervical vertebrae (Gupta 1966; VanBuren and Evans 2017). Similarly, large-headed and/or fully aquatic species (elephants, large bovids, cetaceans, and dugongs) are also characterized by relative long vertebrae in the cranial most region of their cervical spine (Fig. 7). C1 length is strongly increased to transfer the load of the massive head or to resist water pressure. This third group confirms the allometric pattern of C1 recovered by the bivariate analyses. In some cetaceans, this is enhanced by cervical coossification, which prevents uncontrolled head movements caused by water pressure during swimming (Slijper and Harrison 1979; Buchholtz 2001; VanBuren and Evans 2017). Head motion relative to the axial skeleton is furthermore restricted by powerful suboccipital muscles and shortening of C2–C7 (Schulte and Smith 1918; Howell 1930).

These examples reveal that variations in cervical construction are associated with extreme loading conditions. Nevertheless, cervical proportions describe a trilateral continuum of variation across mammals (Fig. 6). The deviations from the general pattern represent the three extrema of the variation. Bivariate relationships between the individual vertebrae and body size are, however, strongly impacted by these species with extreme neck loading regimes. Much of the variation in cervical spine length, as well as in the individual vertebral lengths and proportions, is found in cetartiodactyls, due to the high degree of differentiation of neck morphology and function found in this lineage (neck length, skull and appendages morphology, feeding and locomotor habits) (see Vislobokova 2013).

BIOMECHANICAL DETERMINANTS OF CERVICAL ORGANIZATION

The general construction and internal organization of the cervical spine is strongly based on the divergent scaling of C1 compared to C2–C7, which is shared by almost all mammals. However, the fact that the muskox (*Ovibos moschatus*; proportions of the individual vertebrae (%) on the whole cervical spine = 17:21:14:13:13:11:11) has almost the same cervical vertebra proportions as the garden dormouse (*Eliomys quercinus*; 16:21:14:13:12:11:13) shows that there are no universal rules relating the cervical spine construction to body size, habitat, and locomotion. The low variability of cervical internal organization (under nonextreme loading regimes) raises questions about the role of individual vertebra proportions in neck functions. From a biomechanical point of view, the cervical spine is uniformly constructed across mammals. It constitutes a loaded beam that is supported at one end only (i.e., a cantilever) (Kummer 1959a,b). The weight of the head permanently induces stresses (tension and compression) on the neck. As a result, the head tends to collapse downward in an unbraced condition (Martin et al. 1998). Unlike in birds and long-necked sauropods, head/neck support in mammals is complicated by the efficient masticatory apparatus (notably involving the important weight of the masticatory muscles). To counteract cervical stresses, passive (nuchal and spinal ligaments) and active (dorsal neck muscles) elements stretch from the anterior region of the trunk to the head and the cervical vertebrae. As the nuchal elements completely compensate the neck bending moment to allow the head and neck to maintain their posture, the cervical vertebrae are under purely axial load (Kummer 1959a,b). This general construction limits variation in the length of vertebral centra, the major load bearing structures (Slijper 1942; Kummer 1959a,b; Smit 2002). Consequently, a similar internal organization of the neck is found in most mammals, even if they have quite different neck lengths and/or different locomotor and foraging modes. Our findings confirm the conclusions of Badlangana et al. (2009) that variation in neck lengths in ungulates does not necessarily involve variation in cervical internal organization. However, this principle is now extended to mammals in general. Only under extreme loading regimes of the neck (e.g., massive heads, extremely long necks, fully aquatic and fossorial lifestyle), internal organization is modified to accompany exceptional mechanical requirements. Cervical proportions seem to be adjusted to high craniocervical mobility (Graf et al. 1995a,b), but also to reduce kinematic redundancy (Bizzi et al. 1976; Vidal et al. 1986; Peterson et al. 1989; Keshner 1990; Pellionisz et al. 1991; Graf et al. 1995a; Van Den Berg 2000) within the limits of biomechanical determinants. The surprisingly consistent internal organization of the mammalian cervical spine therefore provides the basis of high functional diversity, despite a relatively low and invariable number of mobile elements.

THE EVOLUTION OF CERVICAL SPINE LENGTH IN MAMMALS

The seven cervical vertebrae rule of mammals is most likely an evolutionary by-product (Gould and Lewontin 1979) of key innovations in mammalian metabolic and locomotor performance (enhanced metabolism, muscularized diaphragm, thoracolumbar differentiation) (Galis 1999; Galis and Metz 2003; Galis et al. 2006; Varela-Lasheras et al. 2011; Buchholtz 2012; Buchholtz et al. 2012; Hirasawa and Kuratani 2013; Buchholtz 2014; Galis et al. 2014; Hirasawa et al. 2016). Thus, the fixed number is unrelated to the craniocervical function itself. Strong negative selection due to the pleiotropic effects of Hox genes in the early development and the strong developmental integration between the cervical region and other body parts (cervical origin of the precursor cells for forelimb and diaphragm muscles) in late development place a strong constraint on the cervical count (see references above). Accordingly, variation corresponding to functional/biomechanical demands are postponed to the late (postnatal) development during vertebral growth (i.e., during the formation of size of the cervical spine as a whole as well as that of the individual vertebrae) (see Bergmann et al. 2006; Van Sittert et al. 2010).

In contrast to its highly determined internal organization, the disparity of overall cervical spine length is the main source of variation of the mammalian neck. We assume that variation in neck length is generally limited by body size due to its biomechanical requirements as a cantilever (as also argued by Kummer 1959a,b). However, the various scaling patterns permit the adjustment of neck length to the demands of head movement and posture (e.g., grooming, mating, drinking, foraging, locomotion, and posture; see Heidweiller et al. 1992) within this limited possible variation. In some species and lineages, natural selection even favored an extreme increase or decrease in neck length. Although maximum neck length in mammals is still not comparable to that of most sauropods (Taylor and Wedel 2013), this mechanism resulted in the extraordinary large range of cervical spine length acquired during mammalian evolutionary diversification (220-fold increase between the Etruscan shrew and the giraffe in our dataset), despite a fixed number of seven vertebrae. Alteration in vertebral count (Buchholtz and Stepien 2009; Hautier et al. 2010; Varela-Lasheras et al. 2011; Buchholtz et al. 2014) actually represents rare and phylogenetically isolated evolutionary events. Alteration of the whole neck length seems to be an important source of cervical variation in mammals, as already suggested by Gans (1992). Due to the combination of large variation in overall length, but limited variation in internal organization, the cervical spine can act as a form–function complex (Bock and Von Wahlert 1965) across the various neck lengths that arose during mammalian evolutionary diversification.

Conclusion

Neck length modification has been crucial in mammalian body size evolution. The developmentally fixed number of cervical vertebrae, however, limits evolutionary modifications in neck length in mammals when compared to birds or sauropods (Van Der Leeuw 1991; Galis 1999). Here, we revealed the patterns of cervical scaling, which nonetheless permits a great disparity of neck length in mammals. Opposite allometric scalings of C1 and C2–C7 accommodate the increase of neck bending moment with body size. A three-class internal organization of the neck skeleton is found with surprisingly uniformity in the vast majority of mammals. Deviations from this general pattern only occur under extreme loading regimes, associated with particular functional and allometric demands. Our results indicate that the main source of variation in the mammalian neck dwells in the disparity of overall cervical spine length. This allows for adaptive modifications to the various demands associated with different head movements and postures (grooming, mating, locomotion, posture, and foraging). The mammalian neck reveals how evolutionary disparity manifests itself in a structure that is otherwise highly restricted by meristic constraints.

AUTHOR CONTRIBUTIONS

PA designed the study, collected all data, and drafted the manuscript. PA and EA conducted all analyses. PA, EA, and MSF interpreted the data and reviewed the manuscript. The authors declare they have no conflicts of interest.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Number of specimens, species, and genera included in the study.
Table S2. List of collection specimens included in the study.
Table S3. Data on individual vertebral lengths (mm), overall cervical spine length (mm), tibial length (mm), and body weight (kg).
Table S4. Scaling analysis for log cervical spine length against log body weight for mammals in general, for the main mammalian clades, and at the (super)familial level.
Table S5. Scaling analysis for log cervical spine length and individual vertebral lengths against log tibial length for mammals in general.
Table S6. Scaling analysis for log cervical vertebral length against log body weight for C1–C7 in mammals in general, the main mammalian clades, and on the (super)familial level.
Table S7. Loadings of the phylogenetic informed PCA of vertebral lengths, overall cervical spine length, and body weight (all log-transformed).
Supplementary R File
Supplementary Timetree Nexus File

Chapter 3

Musculoskeletal networks reveal topological disparity in mammalian neck evolution

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The disparity of the neck's musculoskeletal organization across mammals is examined within the novel framework of anatomical network analysis. The results reveal that the limited number of vertebrae in the mammalian neck does not result in the absence of musculoskeletal disparity. However, this disparity evolved late in mammalian history, particularly in parallel with the radiation of certain lineages. The disparity is further fostered by the close integration of the neck and the forelimb during mammalian evolution.

PA designed the study, collected all data, prepared adjacency matrices, constructed the phylogentic time tree, wrote the R script for the relative variability and disparity-through-time analysis, interpreted the results, prepared all figures and the supplementary material, and wrote the manuscript. PA and BEA conducted the phylogenetic analyses. BEA wrote the R script for the network parameter and modularity analyses and contributed to the discussion of the results. MSF provided conceptual help and contributed to the discussion.

Musculoskeletal networks reveal topological disparity in mammalian neck evolution

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Keywords: anatomical network analysis, network theory, forelimb evolution, mammalian cervical spine, sloths, meristic constraints, modularity

Abstract

Background

The increase in locomotor and metabolic performance during mammalian evolution was accompanied by the limitation of the number of cervical vertebrae to only seven. In turn, nuchal muscles underwent a reorganization while forelimb muscles expanded into the neck region. As variation in the cervical spine is low, the variation in the arrangement of the neck muscles and their attachment sites (i.e., the variability of the neck's musculoskeletal organization) is thus proposed to be an important source of neck disparity across mammals. Anatomical network analysis provides a novel framework to study the organization of the anatomical arrangement, or connectivity pattern, of the bones and muscles that constitute the mammalian neck in an evolutionary context.

Results

Neck organization in mammals is characterized by a combination of conserved and highly variable network properties. We uncovered a conserved regionalization of the musculoskeletal organization of the neck into upper, mid and lower cervical modules. In contrast, there is a varying degree of complexity or specialization and of the integration of the pectoral elements. The musculoskeletal organization of the monotreme neck is distinctively different from that of therian mammals.

Conclusions

Our findings reveal that the limited number of vertebrae in the mammalian neck does not result in a low musculoskeletal disparity when examined in an evolutionary context. However, this disparity evolved late in mammalian history in parallel with the radiation of certain lineages (e.g., cetartiodactyls, xenarthrans). Disparity is further facilitated by the enhanced incorporation of forelimb muscles into the neck and their variability in attachments sites.

Background

The increase in locomotor and metabolic performance was one of the most important innovations in the evolution of mammals [1-6]. This innovation, however, was accompanied by an exceptionally low variability in the number of presacral vertebrae compared to other tetrapods (e.g., [7-14]). In fact, the number of cervical vertebrae in mammals is limited to seven, except in extant manatees and sloths [12]. As mammals evolved a new locomotor mode based on an increase in sagittal axial motions, their back and nuchal muscles underwent an anatomical reorganization [15, 16]. The epaxonic muscles (particularly the iliocostalis system) were reduced along with the decrease of lateral axial motion [15, 16]. With the predominance of girdle-limb system as the main propeller in mammals, pectoral muscles also expanded into the dorsal region [15] and were integrated into the head/neck functional unit. Studies on the evolution of the mammalian neck usually have focused on the role of those muscles emigrating from the cervical region during early development [17-20]. In contrast, the muscles that expanded into the neck have been solely investigated for their impact on shoulder and forelimb mechanics (e.g., [21-24]).

Differences in ecology and size resulted in interspecific differences in the posture and mobility of the head in mammals during standing, locomotion, foraging, oral grooming, and other daily activities (e.g., [25-30]). The morphological basis of these differences, however, is poorly understood. Variation of the cervical column length as a whole has recently been shown to be an important factor in generating morphological disparity of the neck in mammals [31]. As a consequence of the limited variability in the number of vertebrae [9, 12] and in vertebral shape [17, 32-35], the disparity of the cervical skeleton alone is still low. Hence, we suggest that interspecific variation in the arrangement of the neck muscles plus their attachment sites on the cervical vertebrae, the skull and other bones (i.e., the variability of the musculoskeletal organization) should be an important source of morphological disparity of the neck across mammals. Although there are numerous descriptions of the myology of the neck region for almost every mammalian family, only a few studies compared the neck muscle arrangement interspecifically in an evolutionary context (e.g., [36-39]). Moreover, these studies compared neck muscles only qualitatively, which prevents the quantification of the differentiation of the neck muscles arrangement. As a consequence, it is currently unknown whether the interspecific variation in muscle attachments actually affected the changes of the musculoskeletal organization of the neck across mammals.

Anatomical Network Analysis (AnNA) provides a novel framework to study the organization of the anatomical arrangement of bones and muscles of anatomical structures (i.e., the connectivity pattern) [40, 41]. Within this framework, bones and muscles are formalized as the nodes of the network, and the physical contacts among them are formalized as the links that connect the network's nodes. Anatomical network models offer a mathematical description of the organization of the body [41]. Through such mathematical formalism we can identify and quantify structural patterns, such as anatomical modules, without *a priori* assumptions about the developmental or functional factors causing them [40] (for a recent review on morphological modularity see [42]). This allows direct phylogenetic comparisons. In this context, AnNA has been used, for example, to infer evolutionary trends in the skull of tetrapods [43] and the phylogenetic relation between morphological complexity and modularity in the skull of primates [44]. AnNA formalization also allows combining information on skeletal and muscular tissues: in this context, AnNA has been used, for example, to study congenital musculoskeletal malformations [45], secondary injuries [46] in humans, and hindlimb functional integration in frogs [47].

We can also use network parameters as proxies to infer the morphological organization of the body. Table 1 summarizes the network parameters used in this study and their most common morphological interpretation. Further details on the interpretation of network concepts in a morphological context and their historical roots have been given elsewhere (see, e.g., [41, 43, 48-50]). In short, every interpretation derives from the biological role of connections in the network model: what is that connections do? Broadly speaking, the connections we have modeled among the bones and muscles of the neck embody functional interactions (e.g., determining the range of neck motion), as well as developmental factors (e.g., those inducing muscles to attach to a specific vertebrae and not to other). Thus, for example, the number of such connections for a given element, or for the entire network (i.e., K), represents the amount of functional and developmental dependences of this element or of the whole network. Functional and developmental dependences are often associated to Rupert Rield's concept of burden, or more generally, to the concept of constrain of body parts [40, 51-53]. Morphological interpretation of more elaborated network parameters, such as the density of connections (D), the mean clustering coefficient (C), and the mean shortest path length (L), follow a similar logic. Because connections represent biological interactions among anatomical parts, their relative amount (D) serves as a proxy of the complexity available to the system (e.g., to perform complex functions). In addition to quantifying the amount of connections, the way connections are set (e.g., creating intertwined patterns such as 3-node loops (C)) and their effects on topology (e.g., increasing the effective proximity of elements to interact together (L)) also have consequences in the overall integration of the anatomy. Thus, the greater the intertwining, the greater the integration; the closer the elements, the greater the integration. Moreover, differences in the amount of connections among the elements of the network (some have many, most have a few) introduces heterogeneity in the organization of the network. Such heterogeneity can be related before to structural disparity (or anisomerism *sensu* Gregory [43, 54]). Finally, the overall patterns of integration and heterogeneity among the parts of a network often results in the emergence of new properties, for example, modularity [48] (see [55-58] for general reviews on the origin and macroevolution of modularity at a morphological level). The more specific details of the modular organization of a network need a closer observation, but the overall degree of parcellation of the network into large, uniform modules (P) captures how much modular the neck is.

Here we applied AnNA to a phylogenetically broad dataset of mammalian necks, including all bones (cervical vertebrae, cranium, sternum, hyoid and pectoral girdle) and muscles involved in the motion of the head and neck (Fig. 1A-F). First, we modeled the neck of each species as a network in which nodes represented the aforementioned bones and muscles and links represented their physical arrangement or contacts. Then, we quantified seven network parameters that serve as proxies for the morphological organization of the neck anatomy (Table 1). Finally, we explored the disparity of neck musculoskeletal organization through time to answer, specifically: 1) whether the musculoskeletal organization (as captured by network parameters) of the neck really differs among mammals; 2) whether closely related species share similar network organization; 3) whether there is a consistent pattern of modularity across mammalian necks; 4) how extreme elongation and deviating vertebral numbers alter neck organization; and 5) how neck disparity changed during mammalian evolutionary history.

Results

Network parameters and phylogenetic signal

The values of the network parameters used as proxies for the musculoskeletal organization of the neck for individual taxa are listed in Table 2. The phylogenetic signal is statistically significant for the multivariate dataset of all network parameters (Kmult = 0.89, p = 0) as well as for five individual of the seven parameters (N, K, D, H, P; Table 3, additional file AF1). This suggests similar variation in neck organization in closely related species (Fig. 2). A Brownian motion model of evolution best explains trait evolution of the network parameters (see additional file AF1). Relative variability in connectivity *K*, complexity *D*, and integration by co-dependency *C* is high among the species examined (significant higher coefficients of variation; Msrl = 139.58, $p = 0$) (Table 3, additional file AF1). In contrast, relative variability of integration by effective proximity *L*, anisomerism *H*, and the degree of modularity *P* are low across all mammals (Table 3, additional file AF1). There is no significant relationship between the network parameters and either body mass ($F = 0.170$, $p = 0.68$), absolute neck length ($F = 0.005$, $p = 0.94$), relative neck length ($F = 0.661$, $p = 0.42$), or predatory behavior (i.e., predatory vs. non-predatory; $p = 0.46$).

The number of anatomical elements *N* is low in monotremes compared to the general pattern of therians (Fig. 2A). However, most xenarthrans, the chiropterans, and the Pygmy sperm whale (*Kogia breviceps*) also have a decreased number of elements in their neck network. The number of anatomical connections *K* is uniformly high in marsupials in contrast to most other mammals (Fig. 2B). *K* is decreased in monotremes, xenarthrans, chiropterans, the Pygmy sperm whale and the Bactrian camel (*Camelus bactrianus*). Morphological complexity *D* is high in monotremes, intermediate in marsupials and xenarthrans and tends to decrease in most of the other placental lineages (Fig. 2C). For H, the largest contrast can be found between monotremes (very low H) and therians in general, whereas the pattern within therians is not uniform (Fig. 2D). The degree of modularity *P* is relatively invariable and only slight decreases can be found in diprotodonts, Pen-tailed treeshrew (*Ptilocercus lowii*), chiropterans and eulipotyphlans (Fig. 2E). The phylomorphospace (Fig. 3) highlights the differences in neck musculoskeletal organization between monotreme and therian mammals ($\lambda = 4.18$, $p = 0.001$). Marsupials cluster closely together. They slightly overlap with the distribution of placental mammal, which occupy a huge part of the morphospace. The Pygmy sperm whale is far from the other placental mammals.

Community structure and phenotypic modules in neck networks

The number and constitution of the connectivity modules in the neck varies among the mammalian species examined (a summary is given in Table 4; for detailed information see additional file AF1). In many cases however, module number varies based on a left-right split of modules that are united in other species (e.g., the pectoral elements are separated in left and right modules). Overall, five principal connectivity modules were detected: 1) cranio-pectoral, 2) ventral, 3) mid-cervical, 4) lower cervical, and 5) thoracic. This pattern is exemplified here for the lesser grison (*Galictis cuja*) (Fig. 1G). The cranio-pectoral module (present in 32 out of 48 taxa) groups the cranium, the C1, and the bones of the pectoral girdle (scapulae, claviculae, and, if included, humeri), as well as the suboccipital, cleidocephalic (or cephalohumeralis), atlantoscapularis, capital longus, and capital rhomboid muscles. The ventral module groups the sternum, hyoid, thyroid, mandible (when included), and the sternocephalic and infrahyoid muscles. In 32 out of 48 cases, ribs and the related scalenii muscles are also included in this module. The ventral module is combined with (parts of) the pectoral bones and muscles in 15 species, none of which are aclaviculate (Fig. 4B). The mid-cervical module groups C2 to C4 as well as the longus cervicis, spinalis, and their related interspinal, intertransversarii, and multifidii muscles. The lower cervical module groups C5 to C7 with the cervical longissimus, spinalis, and their related interspinal, intertransversarii, and multifidi muscles. These mid-cervical and lower cervical modules are present in all networks (Fig. 4A-D). The border between them is, however, shifted in some species (e.g., C4/C5 to C3/C4). If the attachments of scalenii muscles are limited to few specific cervical vertebrae, these muscle and the ribs are also included in the mid or lower cervical module. The thoracic module groups the thoracic spine, nuchal ligament, semispinalis (complexus + biventer cervicis), capital longissimus, cervical rhomboid and trapezius muscle.

In several species, the pectoral bones (plus the related muscles) are not grouped together with the cranium and C1 but separated; otherwise they are included in the ventral or thoracic module, respectively. For instance, in the long-necked camel the pectoral bones and muscles constitute a distinct module together with the nuchal ligament (Fig. 4C). In the giraffe (*Giraffa camelopardalis*), attachment sites of the pectoral muscles are shifted proximally to the midcervical module. In contrast, the pectoral bones and muscles are combined with the ventral elements into a ventro-pectoral unit in the parti-colored bat (*Vespertilio murinus*) (Fig. 4B). The sloths differ in the organization of their neck due to their aberrant number of cervical vertebrae. In the two-toed sloth (*Choloepus didactylus*; six cervical vertebrae), the pectoral elements form a separate module. The C5, C6, thoracic spine, and related muscles are grouped within one module. In the three-toed sloth (*Bradypus tridactylus*; nine cervical vertebrae; Fig. 4D), there is an upper (C2-C5) and lower (C6-C7) midcervical module. The evolutionary 'new' vertebrae C8 and C9, however, are grouped with the thoracic spine, scapulae, and related muscles. The claviculae are included in the ventral module. The ribs are grouped with the cranium and atlas in the Pygmy sperm whale.

Disparity in neck organization through time

The mean subclade disparity values for the observed and simulated data were plotted against node age (Fig. 2F). Subclade disparity through time is low, which is particularly obvious in the first two-thirds of mammalian evolution (i.e., during the Mesozoic). However, it is not significantly different from the expectation under a Brownian motion model of neck organizational evolution (morphological disparity index = 0.016, p = 0.65). Nevertheless, major shifts in disparity rate occurred in the middle to late Paleocene and in the middle to late Eocene. These shifts resulted in disparity peaks exceeding the 95% confidence interval of the simulated data. The disparity in neck musculoskeletal organization decreased after the Eocene-Oligocene border. A larger sample size would be required to infer significant results for the post-Eocene ages (i.e., more divergence events are needed).

Discussion

Variation in neck organization across phylogeny

The more conserved network parameters (L, H, P) represent measurements of the neck's integration by effective proximity, anisomerism, and degree of modularity [41, 43]. These measurements capture how distant parts of the neck (e.g., head and trunk, lower and upper cervical column) are integrated, that anatomical connections are not evenly distributed across bone (e.g. vertebrae) and the way the neck is modularized. Thus, our results indicate a basic constructional set-up of the neck across mammals determined by morphological regionalization (see further below). These conserved features likely arise due to shared developmental [8, 9, 17, 19, 59-61] and/or biomechanical/constructional constraints [31, 62, 63]. However, the musculoskeletal organization of the neck is not uniform for other morphological features captured by network proxies. Specifically, mammalian necks considerably vary in terms of their morphological burden, complexity, and integration by co-dependency (quantified by K, D, and C, respectively). These features describe the grade of specialization in the neck due to reduction of elements or enhancement of passive structures (e.g., the nuchal ligament) and the way the neck is structurally constrained by the setup up of its muscular connections (i.e., its evolvability) [43, 49]. The variation arises from the major trends of epaxonic muscle modification during mammalian evolution, leading to differences in nuchal muscle organization among monotremes, marsupials and therians. Our findings confirm the plesiomorphic pattern of epaxonic neck muscle arrangement in monotremes [64-67]. It results in a musculoskeletal organization that is distinctively different from that of therian mammals (Fig. 3). Their low differentiation within the three longitudinal systems (longissimus, iliocostalis, transversospinalis; in particular the deep intervertebral muscles; low number of muscles) and muscle attachments that are evenly distributed among the vertebrae (high complexity but low irregularity) suggest low specialization to specific neck motion patterns. In marsupials, epaxonic muscles are more differentiated in deep and superficial layers. Moreover, most of the superficial muscles are attached to every cervical vertebra [66, 68-72]. This high connectivity results in structural constraints in the neck (i.e., morphological burdens) and low musculoskeletal disparity among marsupials in comparison to placentals (Fig. 3). Attachments of epaxonic neck muscles are very variable among placental mammals [70] and thus network parameters are as well. However, two major trends in neck evolution have been shown: First, there is a reduction of attachment sites of the neck muscles to only a few vertebrae/the skull; and second, there is an increased bracing of the head-trunk distance by ligamentous structures to accommodate for increasing head weight and neck length [15, 73-78]. This results in placental mammals generally having necks that are less complex compared to monotreme and marsupial mammals. For instance, few but specialized muscles have the small attachment sites and are able to induce a similar motion or the superficial epaxonic muscles attach only secondarily to the head via the nuchal ligament. In addition, neck variation in placental mammals is also highly influenced by variation in the organization of pectoral bones and muscles (see below).

The phylogenetic signal of most of the network parameters reveals that phylogenetic relationship accounts for much of the variation in neck organization. At the same time, network parameters also discriminate between monotreme, marsupial, and placental mammals. Within placental mammals, however, variation of network parameters is mostly limited to xenarthrans, chiropterans, and some cetartiodactyls. Although relatively species-poor, xenarthrans, show highly specialized neck morphologies related to their diverse fossorial or arboreal ecologies [79-81] and unique development [33, 82, 83]. In chiropterans, back muscles contribute only marginally to the stabilization of the head because of the lack of most cranial and cervical attachments [84-86]. Sagittal stability is instead achieved by the modified morphology of the cervical vertebrae in accordance with roosting behaviors [87]. Cetartiodactyls have recently been show to exhibit the highest disparity in neck morphology across mammals [31]. It ranges from the very short necks of cetaceans up to the extreme long ones of camelids and giraffids. As a consequence, neck musculoskeletal organization is similarly diverse. Several muscles with cervical attachment are reduced in the Pygmy sperm whale (and other cetaceans) or their attachment is shifted to the skull (e.g. scaleni muscles) and thus head stabilization is increased

[88, 89]. On the other hand, cranial attachments of the dorsal neck muscle are mainly reduced in long necked species, such as the camel and giraffe. Muscle force is instead transferred by the modified nuchal ligament [74, 75, 77]. Surprisingly, neck network parameters in the dugong (*Dugong dugon*), although also being fully aquatic, do not show a similar alteration as in the Pygmy sperm whale. Instead, it closely resembles the Asian elephant (*Elephas maximus*) and other afrotherians (Table 1, Fig. 2).
In accordance with our findings, [90, 91] also showed that the effect of size and prey capture behavior is low in the neck compared to the thoracolumbar region. However, functional interpretations of the results of the analysis of the topological arrangement of parts needs to be inferred on a one to one basis and taking into account the specific ecological context of each taxa.

Regionalization and modularity in the mammalian neck

Despite the relative low and invariant number of neck vertebrae in mammals, several studies have uncovered a tripartite regionalization of the cervical spine based on developmental, morphological, allometric, and functional evidence [17, 25, 31, 32, 91]. Our results have now uncovered a corresponding regionalization of the musculoskeletal organization of the mammalian neck into an upper (cranium, C1), mid (C2-C4), and lower cervical module (C5-C7, in some species also the thoracic spine). This modularity pattern is conserved across mammals despite variations in size, feeding mechanisms, and locomotor modes (indicated by a uniform grade of modularity). This conserved pattern probably arose from the high number of connections between the vertebrae of the same module (or the cranium and C1) resulting in an increase of structural constraints and integration of these elements [40, 49, 52]. However, the boundaries between adjacent modules/regions are not consistent across different studies analyzing the morphology of the neck using different criteria. For example, vertebrae C1 and C2 are not part of the same connectivity module despite their close developmental, functional, and evolutionary relationship [25, 92, 93]. A similar dissociation of C1 and C2 into different regions has been shown for their scaling properties [31] and highlights the role of C2 as a functional mediator between the head joint and the postaxial column (see also [94]). In addition to the three 'inner' axial modules, there are two additional 'outer' modules bridging the distance between the trunk and the head (or the hyoid or upper vertebrae), with a muscular cuff on the dorso-lateral (pectoral) and ventro-lateral side. Many of these muscles were crucial for the evolutionary origin of the vertebrate neck [95, 96].

Neck organization in sloths

In general, a similar regionalization of the neck is observed in both genera of sloths, despite their variation in the number of cervical vertebrae. The evolutionary new C8 and C9 in *Bradypus* and their associated muscles are grouped together with the thoracic spine. This agrees with their thoracic origin and ossification sequence [82]. Conversely, the evolutionary new Th1 provides the basis for the close association of the thoracic vertebral region to C5 and C6 in *Choloepus* neck organization. Divergence of the sloths' necks becomes obvious when including their pectoral bones and muscles in the comparison. Their neck-shoulder arrangement represents two different solutions of locomotor possibilities under common functional constraints [80, 97]. Neck organization and modularity of *Bradypus* resembles those of other long necked species. The resemblance stems from its nearly complete lack of cervical and cranial attachments of the neck/shoulder muscles and its unusual clavicular and shoulder morphology [80, 98-100] (see the unusual lower cervical-thoracic-scapular module in Table 4). The muscles of *Choloepus*, in contrast, are so placed as to offer the greatest possible support dorsally and ventrally to the head as well as to the scapula [80, 98, 101, 102]. Thus, neck organization and modularity is closer to the general pattern as seen in the lesser grison (i.e., pronounced head support, functional connection of head and forelimb) [15].

Evolutionary integration of the neck and the forelimb

The enduring evolutionary and developmental relationship between the neck and the forelimb in mammals (and other amniotes) is well documented (e.g., [17, 19, 20, 95, 96, 103]). This relationship is most obvious in the brachial plexus innervating shoulder and forelimb muscles [104, 105]. However, there is also a strong functional integration between the neck and the forelimb, with several muscles connecting the pectoral girdle and the head/neck (often with repeated slips). Based on this functional connection, the posture and movements of the neck have a crucial influence on the mechanics of the forelimb in terms of gait efficiency, balance, stabilization, ground reaction forces, and kinematics [30, 106-112]. Our findings now highlight the consequences of this integration on the musculoskeletal organization of the neck. Although there is a conserved tripartition of the cervical spine and its associated muscles, the varying contribution of pectoral bones and muscles to different connectivity modules accounts for much of the observable neck disparity across mammals (e.g., see results on sloths). Major shifts in forelimb morphology and function (e.g., mobilization of the pectoral girdle, reduction of the claviculae) [113-115] are associated with increasing decoupling of the pectoral elements from the ventral module and their connection to the cranium and upper cervical region. This coincides with the increased role of head/neck movements on forelimb mechanics during fast and endurance running (i.e., cursoriality) [30, 108]. In mammals with extreme long necks (camel, giraffe), although also being capable of enduring walking, the pectoral bones and muscles are separated from the cranial module. However, it has recently been shown that neck pendulum mechanics and function in long-necked mammals is different compared to actual cursors [108].

Implications for the evolution and disparity of the mammalian neck

The differences in neck organization between monotremes and therian mammals is one of the striking findings of this study. They result in high disparity between them whereas their within-subclade disparity is low during the first two-thirds of mammalian evolution. Accordingly, the disparity of the neck of mammals was low during the Mesozoic (Fig. 2F) [116]. Figure 5 illustrates the major grades of musculoskeletal organization during mammalian neck evolution. Monotreme, marsupial, and placental mammals differ in their degree of epaxonic muscle differentiation and the varying integration of the forelimb muscles. In general, the morphological complexity of the neck decreases from monotremes to placentals (Fig. 5) but disparity increases (Fig. 3)

The therian radiation that followed the K/T mass extinction and the appearance of most of the therian and marsupial (supra)orders during the Paleocene was accompanied by an abrupt increase in neck musculoskeletal disparity after a long period of low neck disparity. This was even associated with the appearance of locomotor and foraging specializations [117] and the diversification in body size (e.g., [118]). The second disparity peak during the Eocene coincides with the radiation and increased diversity of modern placental orders, like cetartiodactyls, perissodactyls, carnivorans, and xenarthrans (see [117] and references therein). Thus, disparity in neck organization emerged relatively late in the long mammalian history and is associated with the origin and radiation of specific lineages.

Conclusion

One of our crucial findings is that the musculoskeletal organization of the neck differs between monotreme, marsupial, and placental mammals (Fig. 5). Moreover, particularly the necks of placental mammals are characterized by a reduced complexity despite their increased disparity in musculoskeletal organization and length. Our network analyses revealed a mosaic complexity and disparity in the musculoskeletal organization of the mammalian neck despite the more obvious meristic (and other) constraints on the cervical spine. Musculoskeletal irregularity, effective proximity, degree of modularity, and the occurrence of three inner/axial regions are conserved features among mammalian necks. Thus, a shared biomechanical construction and common developmental interrelationships not only constrain variation in the cervical spine, but are similarly likely to limit musculoskeletal variability in the neck. The conservation of these traits contrasts, however, with the high variability in morphological burden, integration by co-relation, morphological complexity, and the configuration of the ventral and (cranio-)pectoral module in the neck. The expansion of limb muscles in the cervical region not only facilitated enhanced forelimb mechanics but also increased structural disparity (and thus derived motor patterns and mechanics) in the neck. Thus, we highlight the close integration of the neck and the forelimb during mammalian evolution. The disparity in neck musculoskeletal organization evolved late in mammalian history and in parallel with the radiation of some lineages (e.g., cetartiodactyls, xenarthrans). Finally, our findings show that the limited number of vertebrae in the cervical spine does not necessarily result in low musculoskeletal disparity during mammalian evolutionary diversification.

Material and Methods

Data collection and anatomical network modeling

We collected the topographic data of the musculoskeletal system of the neck in 48 mammalian species through an extensive literature review (Table 2, additional file AF2). The sample represents all major monotreme, marsupial, and placental clades, as well a diversity of locomotor and feeding strategies. Rodent diversity is represented by members of all suborders (sciuromorphs, myomorphs, hystricomorphs, castorimorphs, and anumaluromorphs, respectively). Representatives of both genera of extant sloth (*Bradypus* and *Choloepus*) were included to examine the influence of their deviating number of cervical vertebrae on neck organization. We documented the number and specific connections/attachments of all skeletal structures and muscles constituting the neck motion system in these taxa.

We included all muscles originating from the cervical vertebrae, skull (cranium or mandible), nuchal ligament, or hyoid/thyroid, and inserting on the (cervical or thoracic) vertebrae, sternum, pectoral girdle (scapulae, claviculae, humeri), or ribs (see details in additional file AF3). Accordingly, we excluded the masticatory, facial, laryngeal, pharyngeal, and suprahyoid muscles from the analysis. A calibrated phylogenetic tree was constructed using the data from the Timetree of Life database [119, 120] (Fig. 2).

We built anatomical network models of the necks' musculoskeletal systems, which comprised all anatomical units as well as the different types of physical interaction among them. Network nodes represented all bones (cranium, cervical vertebrae, thoracic spine, left and right ribs, hyoid, left and right claviculae, left and right scapulae, sternum, and, if involved, left and right humeri, and mandible), other passive elements (nuchal ligament, if present, thyroid), and all cervical muscles, as described above. Network connections represented all physical articulations between bones and other passive elements described, as well as the fleshy and tendinous attachments of the muscles onto the bones (see adjacency matrices in additional file AF4). Network models were analyzed using the *igraph* package [121] in R [122].

Network parameter analyses

The mathematical definitions and calculations of the network parameters examined here (*N*, *K*, *D*, *C*, *L*, *H*, *P*) are provided in Table 1. The degree of modularity (parcellation *P*) was measured from the connectivity modules identified using a spin-glass model and simulated annealing algorithm implemented in the R package *netcarto* [123, 124]. A connectivity module is defined as a group of nodes highly connected among them and poorly connected to nodes outside the group. *P* is 0 when all nodes are in a same module, and tends to 1 when nodes are evenly distributed within many modules. We tested the phylogenetic signal in the multivariate dataset of all network parameters by calculating K_{mult} [125] using R package *phylocurve* [126]. We additionally tested the phylogenetic signal of the individual parameters using the Abouheif's test with 1 000 permutations [127] and Blomberg's test [128] in the R package *phytools [129]*. Mode of trait evolution was explored by comparing fits of Brownian motion, Ornstein-Uhlenbeck, and Early burst models using Akaike information criterion (AIC) weights in R package *geiger [130]*. Distribution of the network parameters was visualized with a phylomorphospace of the first two principal components using R package *phytools* [129].

Relative variability of the network parameters was analyzed by statistical comparison of their coefficients of variation (CVs). 95% confidence intervals of the CVs were calculated by 10 000 bootstrap resampling. Significant differences among the parameters' CVs were tested using the modified signed-likelihood ratio test (MSLRT) for equality of CVs (all parameters) and the asymptotic test for the equality of CVs (pair-wise comparisons, Bonferroni corrected) in the R package *cvequality* [131]. In order to test for allometric effects on network parameters they were regressed against logtransformed body mass, absolute neck length, and relative neck length. Body mass and neck length data were taken from [31]. Relative neck lengths were calculated by dividing absolute neck length by body mass$^{1/3}$. Allometric analyses were done using phylogenetic generalized least square regressions in the R package *caper* [132]. The effect of predatory behavior on logtransformed network parameters was examined by testing for significant differences between predatory and non-predatory mammals using nonparametric Manova for small sample sizes with 10 000 permutations in the R package *npmv* [133]. Species were classified as predatory when food intake involves head-neck movements to hold the food counteracting its resisting movements (carnivorous, insectivorous, piscivorous species). In contrast, species were classified as non-predatory when food intake does not involve such head-neck movements (food is just picked or harvested, e.g., browsers, grazers, but also myrmecophagous species). Differences in network parameters between monotreme, marsupial, and placental mammals were tested using nonparametric Manova for small sample sizes with 10 000 permutations and Wilks' Lamda (λ) in the R package *npmv*.

Modularity analysis

We calculated the quality of the partitions identified by the community detection algorithm using the optimization function Q [134]. According to Newman and Girvan [134], if the number of connections within modules is not different from that expected at random, then Q will be close to 0. The higher the Q the stronger the modular pattern of the network (Q_{max}=1). In practice, strongly modular networks show Q values ranging from 0.3 to 0.7 [134]. Thus, we considered that an anatomical network has a strongly modular structure if $Q - Q_{error} > 0.3$. The expected error of Q was calculated using a jackknife procedure, where every link was taken as an independent observation [134] (more details are provided in additional file AF3). Finally, we estimated the statistical significance of each module using a two-sample Wilcoxon rank-sum test on the internal vs. external links of the module's nodes. The null hypothesis was that the number of connections is the same inside as outside the module (i.e., as expected if the module were created at random); the alternative hypothesis was that the number of connections is higher inside than outside the module (i.e., the definition of connectivity module).
An extensive account of these methods has been given elsewhere [41, 48, 135].

Disparity through time analysis

We carried out a disparity through time (DTT) analysis using the R package *geiger* [130] to trace the variation in neck organization through the evolution of mammals. First, we performed a principal component analysis (PCA) of the network parameters used as proxies of the morphological organization of the neck (i.e., *N*, *K*, *C*, *D*, *L*, *H*, and *P*) to account for their co-variation structure. Mean subclade disparity through time for the PC scores were calculated [116, 136]. Observed disparity in neck organization across our phylogeny was compared with that expected under a Brownian motion process performing 10 000 iterations. High disparity values indicate high variance within subclades; low disparity values indicate conservation within subclades and high variance among subclades. Finally, we calculated the morphological disparity index to quantify the overall difference in relative disparity of a clade compared to that expected under the null Brownian motion model [116, 136].

Abbreviations of network elements

Left and right side are indicated by *l* and *r*, respectively, added to the abbreviations.

asd atlantoscapularis dorsalis; *asv* atlantoscapularis ventralis; *bc* biventer cervicis; *C1-C9* cervical vertebrae; *cal* longus capitis; *cc* cleidocervicalis; *cl* clavicle; *cm* cleidomastoideus; *co* cleidooccipitalis; *col* longus colli; *cx* complexus; *cr* cranium; *hu* humerus; *hy* hyoid; *icc* iliocostalis cervicis; *id1-id8* intertransversarii cervicis dorsales; *im1-im4* intertransversarii cervicis mediales; *is1-is8* interspinalis; *iv/iv1-iv8* intertransversarii cervicis ventrales (fused/separate); *lat* longus atlantis; *lca* longissimus capitis; *lce* longissimus cervicis; *ln* nuchal ligament; *m1-m6* multifidi; *md* mandible; *oca* obliquus capitis caudalis; *ocr* obliquus capitis cranialis; *oh* omohyoideus; *rca* rhomboideus capitis; *rce* rhomboideus cervicis; *rci* rectus capitis dorsalis intermedius; *rh* rhomboideus (undifferentiated); *ri* ribs; *rl* rectus capitis lateralis; *rma* rectus capitis dorsalis major; *rmi* rectus capitis dorsalis minor; *rv* rectus capitis ventralis; *sce* spinalis cervicis; *sc* scapula; *scm* sternocleidomastoideus (sternal and clavicle part not separate); *sd* scalenus dorsalis; *sh* sternohyoideus; *sm* scalenus medius; *so* sternooccipitalis; *spca* splenius capitis; *spce* splenius cervicis; *sp* splenius (undifferentiated); *ssca* semispinalis capitis; *ssce* semispinalis cervicis; *st* sternum; *sth* sternothyroideus; *stm* sternomastoideus; *stx* sternomaxillaris; *svc* serratus ventralis cervicis; *sv* scalenus ventralis; *tr* trapezius; *ts* thoracic spine; *ty* thyroid

Declarations

Availability of data and materials

All data generated and analyzed during this study are included in this published article and its supplementary information files.

Competing interests

The authors declare that they have no competing interests.

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Author's contribution

PA and MSF designed the study. PA collected all data and prepared the manuscript and figures. PA and BE-A analyzed the data. All authors interpreted and revised the manuscript. The authors declare that they have no competing interests.

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Additional files

AF1_results.pdf

Additional information on results on phylogenetic, network, and modularity analyses

AF2_ references.pdf

Systematics and references of investigated species

AF3_method.pdf

Additional information on methods

AF4_adjacency matrices.xls

Adjacency matrices coding for the topological information of neck's musculoskeletal organization of investigated species

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Tables

Table 1 Summary of network parameters used in this study

Network parameter	**Mathematical definition**	**Morphological interpretation**
Number of nodes (N)	Direct count of the number of nodes in the network	Number of anatomical elements
Number of links (K)	Direct count of the number of links in the network	Number of anatomical relations (burden or constrain), connectivity
Density of connections (D)	Relative amount of links: $$D = \frac{2K}{N(N-1)}$$	Morphological complexity
Mean clustering coefficient (C)	Relative amount of 3-node loops: $$C = \frac{1}{N}\sum \frac{\sum e_i}{k_i(k_i-1)}$$ where e_i is the existing number of links among the neighbors of node *i* and k_i is the total number of links of a node *i*	Co-dependency (integration)
Mean shortest path length (L)	Average distance between every pair of nodes: $$L = \frac{1}{N-1}\sum d_{n_i,n_j}$$ where *d* is the shortest distance in number of links between a given pair of nodes n_i and n_j	Effective proximity (integration)
Heterogeneity of connections (H)	Disparity in the number of links per node: $$H = \sigma_K/\mu_K$$ where σ_K and μ_K are the standart deviation and mean of *K*, respectively	Anisomerism
Parcellation (P)	Extent and uniformity of the modular division: $$P = 1 - \sum (N_m/N)^2$$ where N_m is the number of nodes in module *m*	Degree of modularity

Table 2 Network parameters of the musculoskeletal organization of the neck of 48 mammalian species.

Order	Species	N	K	D	C	L	H	P
Afrosoricida	*Chrysospalax trevelyani*	112	328	0.053	0.456	2.81	1.448	0.820
	Micropotamogale ruwenzorii	108	329	0.057	0.482	2.771	1.449	0.784
Carnivora	*Canis lupus*	123	368	0.049	0.351	2.714	1.529	0.784
	Civettictis civetta	113	357	0.056	0.468	2.706	1.504	0.767
	Felis silvestris	103	320	0.061	0.452	2.65	1.401	0.784
	Galictis cuja	118	322	0.047	0.448	2.928	1.416	0.780
	Zalophus californianus	118	338	0.049	0.479	2.795	1.43	0.801
Cetartiodactyla	*Babyrousa babyrussa*	106	344	0.062	0.398	2.734	1.409	0.784
	Bos taurus	108	329	0.057	0.41	2.777	1.395	0.789
	Camelus bactrianus	96	232	0.051	0.295	2.903	1.268	0.771
	Giraffa camelopardalis	106	309	0.056	0.435	2.731	1.421	0.793
	Kogia breviceps	96	219	0.048	0.488	3.099	1.316	0.825
Chiroptera	*Pteropus vampyrus*	92	260	0.062	0.452	2.778	1.329	0.732
	Vespertilio murinus	96	264	0.058	0.476	2.821	1.358	0.729
Cingulata	*Dasypus novemcinctus*	95	279	0.062	0.524	2.769	1.331	0.844
Dasyuromorpha	*Sarcophilus harrisii*	118	390	0.056	0.449	2.714	1.502	0.779
Didelphimorphia	*Didelphis virginiana*	108	374	0.065	0.385	2.668	1.413	0.795
Diprotodontia	*Macropus rufus*	112	355	0.057	0.446	2.726	1.425	0.725
	Phascolarctos cinereus	119	397	0.057	0.429	2.699	1.538	0.710
	Trichosurus vulpecula	109	348	0.059	0.402	2.743	1.432	0.725
Eulipotyphla	*Erinaceus europaeus*	104	330	0.062	0.441	2.747	1.419	0.734
	Scalopus aquaticus	108	322	0.056	0.425	2.788	1.439	0.728
	Suncus murinus	104	304	0.057	0.411	2.835	1.418	0.753
Hyracoidea	*Procavia capensis*	115	340	0.052	0.451	2.84	1.507	0.815
Lagomorpha	*Oryctolagus cuniculus*	122	343	0.046	0.422	2.831	1.556	0.786
Monotremata	*Ornithorhynchus anatinus*	84	282	0.081	0.382	2.575	1.179	0.765
	Tachyglossus aculeatus	85	260	0.073	0.389	2.709	1.183	0.791
Notoryctemorphia	*Notoryctes typhlops*	112	363	0.058	0.455	2.736	1.485	0.806
Paucituberculata	*Caenolestes fuliginosus*	122	383	0.052	0.435	2.767	1.544	0.770
Peramelemorphia	*Macrotis lagotis*	120	396	0.055	0.434	2.72	1.541	0.790
Perissodactyla	*Equus caballus*	124	327	0.043	0.454	2.874	1.555	0.774
	Tapirus indicus	114	321	0.05	0.463	2.862	1.463	0.815
Pholidota	*Manis pentadactyla*	101	292	0.058	0.456	2.873	1.375	0.791
Pilosa	*Bradypus tridactylus*	110	318	0.053	0.548	2.909	1.293	0.782
	Choloepus didactylus	90	255	0.064	0.489	2.708	1.339	0.762
	Cyclopes didactylus	96	260	0.057	0.456	2.917	1.319	0.820

Order	Species	N	K	D	C	L	H	P
	Homo sapiens	113	334	0.053	0.512	2.712	1.442	0.793
Primates	*Loris tardigradus*	114	344	0.053	0.352	2.731	1.47	0.808
	Macaca mulatta	122	369	0.05	0.344	2.719	1.504	0.812
Proboscidea	*Elephas maximus*	110	273	0.046	0.439	2.829	1.424	0.797
	Chinchilla lanigera	108	320	0.055	0.404	2.761	1.423	0.831
	Heteromys desmarestianus	96	294	0.064	0.356	2.719	1.256	0.803
Rodentia	*Neotoma fuscipes*	120	333	0.047	0.409	2.825	1.521	0.814
	Pedetes capensis	112	323	0.052	0.434	2.775	1.474	0.802
	Sciurus vulgaris	130	364	0.043	0.421	2.807	1.575	0.780
Scandentia	*Ptilocercus lowii*	114	336	0.052	0.483	2.785	1.49	0.719
Sirenia	*Dugong dugon*	106	310	0.056	0.505	2.782	1.413	0.795
Tubulidentata	*Orycteropus afer*	101	272	0.054	0.504	2.86	1.308	0.783

N Number of elements; *K* Number of connections; *D* Density of connections; *C* Mean clustering coefficient; *L* Mean shortest path length; *H* Heterogeneity of connections; *P* Parcellation index

Table 3 Variability and phylogenetic signal in neck network parameters.

	N	K	D	C	L	H	P
Minimum	84	219	0.043	0.295	2.575	1.179	0.71
1st Quartil	102.5	293.5	0.052	0.41	2.72	1.371	0.769
Mean	108.6	321.5	0.056	0.437	2.782	1.421	0.782
3rd Quartil	115.8	345	0.058	0.464	2.83	1.493	0.802
Maximum	130	397	0.081	0.548	3.099	1.575	0.844
Coefficient of Variation	0.097	0.132	0.128	0.114	0.031	0.066	0.04
95% Confidence Intervalls	0.077/0.115	0.104/0.155	0.092/0.16	0.085/0.138	0.022/0.04	0.051/0.079	0.032/0.047
Abouheif's Cmean	0.372***	0.421***	0.366***	0.133	0.172	0.359***	0.354***
Blomberg's K	0.995***	0.879***	1.479***	0.559	0.762	1.108***	0.719**

N Number of elements; *K* Number of connections; *D* Density of connections; *C* Mean clustering coefficient; *L* Mean shortest path length ; *H* Heterogeneity of connections; *P* Parcellation index. Significance levels of the tests for phylogenetic signal: p<0.01**; p<0.001***

Table 4 Summary of network modules

Order	Species	M1	M2	M3	M4	M5
Afrosoricida	*Chrysospalax trevelyani*	**cranio-atlantal pectoral**	midcervcial	lower cervical - thoracic	ventral	
	Micropotamogale ruwenzorii	cranio-atlantal	midcervcial[a]	lower cervical - thoracic	ventral	**pectoral**
Carnivora	*Canis lupus*	**cranio-atlantal pectoral**	midcervical	lower cervical	ventral	thoracic
	Civettictis civetta	**cranio-atlantal pectoral**	midcervcial	lower cervical - thoracic	ventral	
	Felis silvestris	**cranio-atlantal pectoral**	midcervcial	lower cervical	ventral	thoracic
	Galictis cuja	**cranio-atlantal pectoral**	midcervcial	lower cervical	ventral	thoracic
	Zalophus californianus	cranio-atlantal	midcervcial	lower cervical - thoracic	ventral	**pectoral**
Cetartiodactyla	*Babyrousa babyrussa*	**cranio-atlantal humeral**	midcervical	lower cervical - thoracic	ventral	**scapular**

Order	Species	M1	M2	M3	M4	M5
	Bos taurus	**cranio-atlantal humeral**	midcervcial	lower cervical - thoracic	ventral	**scapular**
	Camelus bactrianus	cranio-atlantal	midcervical	lower cervical - thoracic	ventral	**pectoral**
	Giraffa camelopardalis	cranio-atlantal	**midcervcial-pectoral**	lower cervical	ventral	thoracic
	Kogia breviceps	cranio-atlantal costal	midcervcial	lower cervical - thoracic	ventral	**pectoral**
Chiroptera	*Pteropus vampyrus*	cranio-atlantal	midcervcial	lower cervical - thoracic	**ventro-pectoral**	
	Vespertilio murinus	cranio-atlantal	midcervcial	lower cervical - thoracic	**ventro-pectoral**	
Cingulata	*Dasypus novemcinctus*	cranio-atlantal axial	midcervcial	lower cervical	ventral	thoracic
Dasyuromorpha	*Sarcophilus harrisii*	cranio-atlantal	midcervcial	lower cervical - thoracic	ventral	pectoral
Didelphimorphia	*Didelphis virginiana*	**cranio-atlantal pectoral**	midcervcial	lower cervical - thoracic	ventral	
Diprotodontia	*Macropus rufus*	**cranio-atlantal pectoral**	midcervcial	lower cervical - thoracic	ventral[d]	
	Phascolarctos cinereus	**cranio-atlantal pectoral**	midcervcial	lower cervical - thoracic	ventral	
	Trichosurus vulpecula	**cranio-atlantal pectoral**	midcervcial	lower cervical - thoracic	ventral	
Eulipotyphla	*Erinaceus europaeus*	**cranio-atlantal pectoral**	midcervcial	lower cervical - thoracic	ventral	

Order	Species	M1	M2	M3	M4	M5
	Scalopus aquaticus	**cranio-atlantal pectoral**	midcervcial	lower cervical - thoracic	ventral	
	Suncus murinus	atlantal	midcervcial	lower cervical - thoracic	**cranio-ventro-pectoral**	costal
Hyracoidea	*Procavia capensis*	**cranio-atlantal pectoral**	midcervcial	lower cervical	ventral	thoracic
Lagomorpha	*Oryctolagus cuniculus*	**cranio-atlantal pectoral**	midcervical[b]	lower cervical - thoracic	ventral	
Monotremata	*Ornithorhynchus anatinus*	cranio-atlantal	midcervcial	lower cervical - thoracic	**ventro-pectoral**	
	Tachyglossus aculeatus	cranio-atlantal axial	midcervcial	lower cervical - thoracic	ventral	**pectoral**
Notoryctemorphia	*Notoryctes typhlops*	cranio-atlantal	midcervcial	lower cervical	**ventro-pectoral**	thoracic
Paucituberculata	*Caenolestes fuliginosus*	**cranio-atlantal pectoral**	midcervical[c]	lower cervical - thoracic	ventral	
Peramelemorphia	*Macrotis lagotis*	**cranio-atlantal pectoral**	midcervcial[a]	lower cervical - thoracic	ventral	
Perissodactyla	*Equus caballus*	**cranio-atlantal pectoral**	midcervcial	lower cervical	ventral	thoracic
	Tapirus indicus	**cranio-atlantal pectoral**	midcervcial	lower cervical	ventral	thoracic
Pholidota	*Manis pentadactyla*	**cranio-atlantal pectoral**	midcervical[b]	lower cervical - thoracic	ventral	
Pilosa	*Bradypus tridactylus*	cranio-atlantal	upper midcervical	lower midcervical	**ventro-clavicular**	**lower cervical - thoracic scapular**

Order	Species	M1	M2	M3	M4	M5
	Choloepus didactylus	cranio-atlantal	midcervcial	lower cervical - thoracic	ventral	**pectoral**
	Cyclopes didactylus	cranio-atlantal	midcervcial - thoracic	lower cervical C5&rest	ventral	**pectoral**
Primates	*Homo sapiens*	cranio-atlantal	midcervical[b]	lower cervical - thoracic	ventral	**pectoral**
	Loris tardigradus	**cranio-atlantal pectoral**	midcervcial[a]	lower cervical - thoracic	ventral	thoracic
	Macaca mulatta	**cranio-atlantal pectoral**	midcervical[c]	lower cervical - thoracic	ventral	costal
Proboscidea	*Elephas maximus*	**cranio-atlantal pectoral**	midcervical[c]	lower cervical - thoracic	ventral	
Rodentia	*Chinchilla lanigera*	**cranio-atlantal scapular**	midcervical	lower cervical	**ventro-clavicular**	thoracic
	Heteromys desmarestianus	cranio-atlantal	midcervcial	lower cervical - thoracic	ventral	**pectoral**
	Neotoma fuscipes	**cranio-atlantal pectoral**	midcervical	lower cervical - thoracic	ventral	
	Pedetes capensis	**cranio-atlantal pectoral**	midcervcial[a]	lower cervical - thoracic	ventral	
	Sciurus vulgaris	**cranio-atlantal scapular**	midcervcial	lower cervical - thoracic	**ventro-clavicular**	
Scandentia	*Ptilocercus lowii*	**cranio-atlantal pectoral**	midcervcial	lower cervical - thoracic	ventral	

Order	Species	M1	M2	M3	M4	M5
Sirenia	*Dugong dugon*	**cranio-atlantal pectoral**	midcervcial	lower cervical	ventral	thoracic
Tubulidentata	*Orycteropus afer*	**cranio-atlantal pectoral**	midcervical[b]	lower cervical - thoracic	ventral	

Contribution of the pectoral elements to different modules marked in bold. Left-right division of pectoral and costal elements is not considered in this summary table. Scapular. humeral. and clavicular elements are separately indicated when the pectoral bones and associated muscles are not group within the same module.

[a] no clear assignment of C5 to the midcervical or lower cervical module

[b] potential subdivision of the midcervical module into C2/C3 and C4/C5

[c] no clear assignment of C2 to the cranio-atlantal or midcervical module

[d] no clear division between the cranio-atlantal and ventral module

Figures

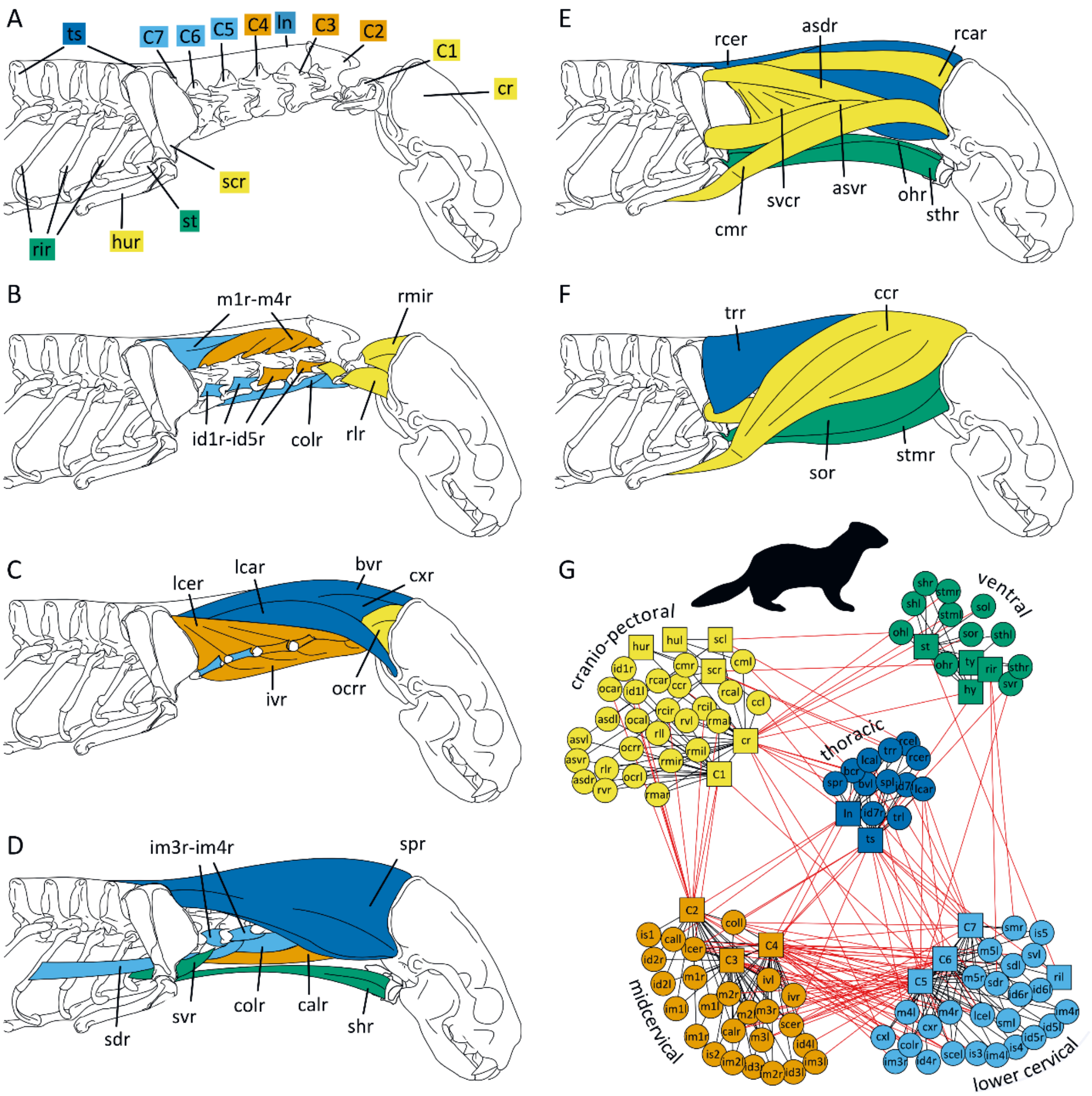

Figure 1 Musculoskeletal anatomy of the neck in the lesser grison (*Galictis cuja*) and its translation into the anatomical network.

(A) Skeletal and (B-F) muscular elements included in the analysis (from deep to superficial). (G) Anatomical network representing the same topological information. Colors code for the identified connectivity modules. Red links between-modules. black links within modules. (A-F) modified after [137, 138].

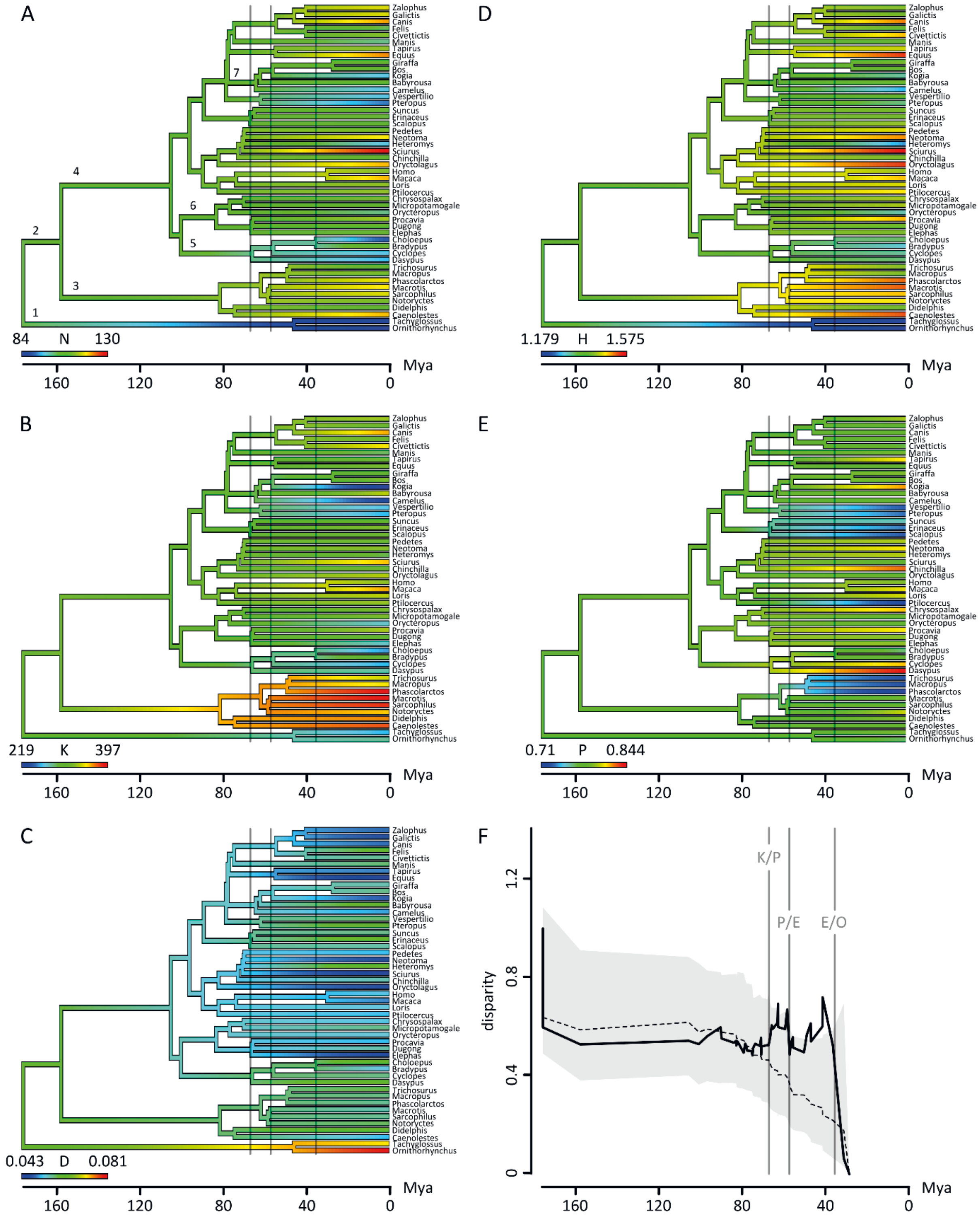

Figure 2 Phylogenetic signal and disparity through time (DTT) for neck network parameters across mammals.

(A) Number of elements *N*; (B) Number of connections *K*; (C) Density of connections *D*; (D) Heterogeneity of connections *H*; (E) Parcellation index *P*; (F) mean subclade disparity through time plot. Gray. vertical lines indicate Cretaceous-Tertiary (K/T). Paleocen-Eocene (P/E). and Eocene-Oligocene (E/O) boundary. Numbers indicate selected taxa: 1 Monotremata: 2 Theria; 3 Marsupialia; 4 Placentalia; 5 Xenarthra; 6 Afrotheria; 7 Cetartiodactyla. In (F). the solid line indicates actual median subclade DTT of the sample. The dashed line indicates the median subclade DTT based on 10 000 simulations of character evolution under Brownian motion. The shaded area indicates the 95% DTT range for the simulated data.

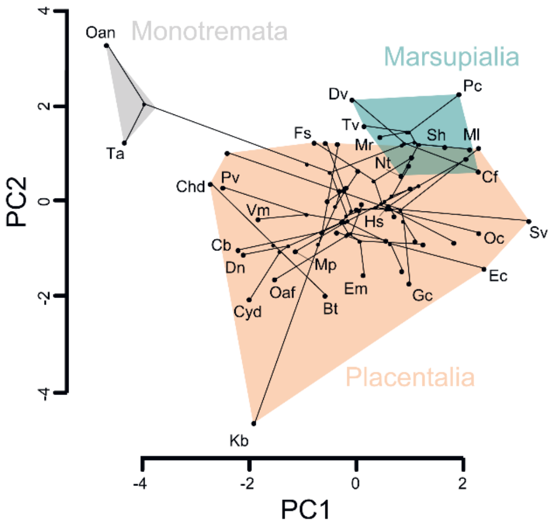

Figure 3 Phylomorphospace of the network parameters

Monotreme, marsupial and selected placental species are labeled. Species abbreviations: Bt *Bradypus tridactylus*; Cb *Camelus bactrianus*; Cf *Caenolestes fuliginosus*; Chd *Choloepus didactylus*; Cyd *Cyclopes didactylus*; Dn *Dasypus novemcinctus*; Dv *Didelphis virginiana*; Ec *Equus caballus*; Em *Elephas maximus*; Fs *Felis silvestris*; Gc *Galictis cuja*; Hs *Homo sapiens*; Kb *Kogia breviceps*; Ml *Macrotis lagotis*; Mp *Manis pentadactyla*; Mr *Macropus rufus*; Nt *Notoryctes typhlops*; Oaf *Orycteropus afer*; Oan *Ornithorhynchus anatinus*; Oc *Oryctolagus cuniculus*; PC *Phascolarctos cinereus*; Pv *Pteropus vampyrus*; Sh *Sarcophilus harrisii*; Sv *Sciurus vulgaris*; Ta *Tachyglossus aculeatus*; Tv *Trichosurus vulpecula*; Vm *Vespertilio murinus*;

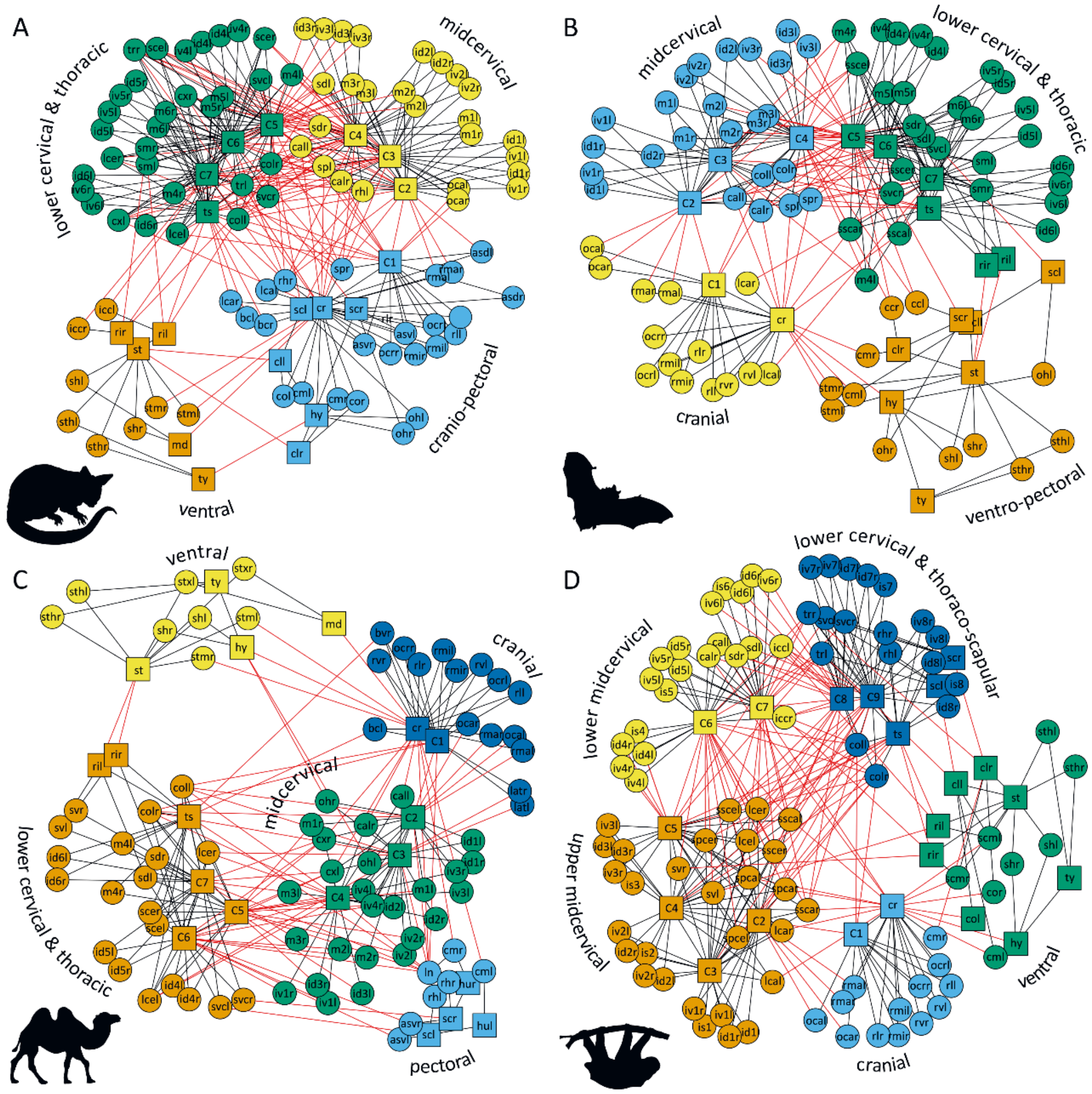

Figure 4 Network representations and connectivity modules of the neck of different mammals.

(A) Common brushtail possum (*Trichosurus vulpecula*); (B) Parti-coloured bat (*Vespertilio murinus*); (C) Bactrian camel (*Camelus bactrianus*); (D) Three-toed sloth (*Bradypus tridactylus*). Colors code for the identified connectivity modules. Red links between-modules. black links within modules.

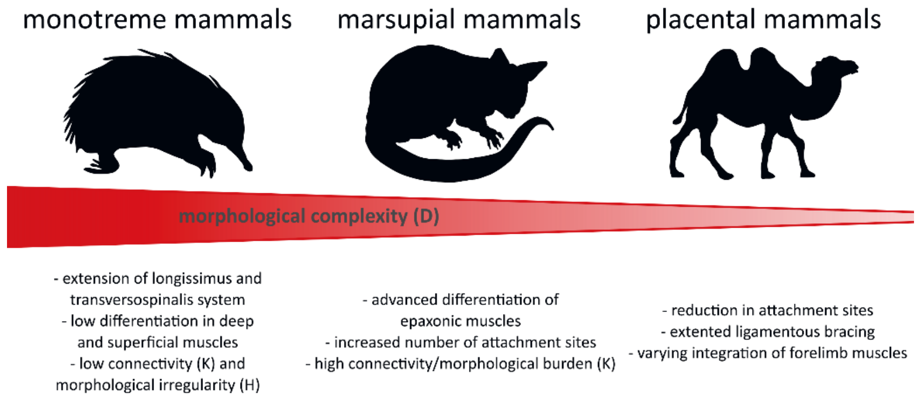

Figure 5 Differences in the musculoskeletal organization of the neck between monotreme. marsupial. and placental mammals.

In general. the morphological complexity of the neck (estimated by the density of connections D) decreases from monotreme to placental mammals (red bar) despite the disparity in neck organization and neck length among the latter.

Chapter 4

Mammalian Hox code and morphological modularity: homeotic transformations explain departure from mammalian 'rule of seven' in sloths

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Sloths are one of the only two exceptions to the mammalian 'rule of seven' cervical vertebrae in the neck. Two competing hypotheses have been proposed, both requiring Direct evidence supporting the either hypothesis would involve knowledge of the vertebral *Hox* code in sloths to be tested. Basing on the previously established correlation between anterior *Hox* gene expression and the quantifiable vertebral shape, the results suggest a mouse-like *Hox* code in the neck of sloths with an anterior or posterior shift of *HoxC-6* expression in association with the first thoracic vertebra in short- or long-necked sloths, respectively. These observations support the homeosis hypothesis of the sloths' neck and suggest a conserved modular pattern as the genetic mechanisms in the evolution of the vertebral column in mammals.

CB and JAN designed the study. CB did the analysis, interpreted the data and drafted the manuscript. EA, PA and AHvH collected the data. CB, PA and JAN prepared the figures. All authors contributed to the discussion and the final manuscript version.

Hox code and morphological modularity: homeotic transformations explain departure from the mammalian 'rule of seven' in sloths

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Running title: *Hox* code in sloths

Keywords: axial patterning, *Hox* genes, evolution, constraint, Xenarthra, cervical vertebrae

Abstract

Sloths are one of the only two exceptions to the mammalian 'rule of seven' vertebrae in the neck. Although a striking case of breaking the evolutionary constraint, the explanation for the exceptional number of cervical vertebrae in sloths is still under debate. Two competing hypotheses have been proposed: (1) the homeosis hypothesis which involves morphological transformation of vertebrae due to changes in the *Hox* gene expression pattern and (2) the primaxial/abaxial repatterning hypothesis which assumes a shift of the pectoral girdle and limbs relative to the non-altered vertebrae. Direct evidence supporting the either hypothesis would involve knowledge of the vertebral *Hox* code in sloths, but the realization of these studies is extremely limited.

Here, on the basis of the previously established correlation between anterior *Hox* gene expression and the quantifiable vertebral shape, we present the morphological regionalization of the neck in three different species of sloths with aberrant cervical count. Our results suggest a mouse-like *Hox* code in the neck of sloths with an anterior shift of *HoxC-6* expression in association with the first thoracic vertebra in short-necked sloths with decreased cervical count, and a posterior shift of *HoxC-5* and *HoxC-6* expression in long-necked sloths with increased cervical count. These observations support the homeosis hypothesis and provide a reliable quantitative basis for further research including fossil taxa such as extinct 'ground sloths' in order to trace the pattern and the underlying genetic mechanisms in the evolution of the vertebral column in mammals.

Significance statement

Understanding the evolutionary origin of biodiversity is a fundamental challenge in biology. Recent research has shown that, in addition to Darwinian variation and selection, the function of regulatory genes during development plays a major role in the evolution of disparate morphologies. Changes in these genes, however, can be associated with side effects that dramatically lower fitness, and thus may indirectly constraint evolutionary change. The constant number of seven cervical vertebrae in mammals represents such a compelling case of evolutionary stability. Studying the only exceptions to this conservation of body plans (i.e., sloths and manatees) will provide insights into the evolutionary mechanisms responsible for the constraints that are imposed on the morphological adaptability of the cervical vertebral column in mammals.

Introduction

The mammalian 'rule of seven' vertebrae in the neck is a striking case of evolutionary stability (1-3). Remarkably, sloths (Xenarthra) and manatees (Sirenia) depart from other mammals by displaying either reduced or increased cervical counts and, in case of sloths, considerable intraspecific variation in the number of cervical vertebrae (CV) (1, 4-8). Analysis of these exceptions will further our understanding of the evolutionary conservatism in the mammalian axial skeleton.

The two living, distantly related genera of sloths are superficially similar (folivorous, arboreal, upside-down posture, suspensory locomotion) (9), but two-toed sloths (*Choloepus*) have five to seven CV while three-toed sloths (*Bradypus*) have eight to nine CV (3-5, 10, 11). *Choloepus* has a relatively short and robust neck and keeps its head upside-down during suspensory postures, whereas *Bradypus*, having a remarkably long and flexible neck, is reported to be able to rotate its head for 270° in both directions (12, 13). The explanation for the exceptional number of CV in sloths is still under debate (1, 4-8), yet a mechanism that allows to break the seven CV constraint is likely to be involved.

A cause for the conservation of body plans, including the constancy of the number of CV in mammals, is argued to be indirect selection due to pleiotropy (e.g., 14, 15, 16). Pleiotropy refers to the phenomenon of mutations in a single gene that affect more than one phenotypic character of an organism (16-18). Changes in pleiotropic genes were found to be associated with effects that dramatically lower fitness (malformations and cancers), and thus may indirectly constrain evolutionary change (e.g., 14, 17, 19). Indeed, skeletons of mammals with an atypical number of CV show many anomalies, such as fusion of vertebrae, defective production of cartilage, ossification of sternum and pelvic girdle, abnormal fibrous bands connected to rudimentary ribs, and asymmetric ribs (1, 4, 20).

Two competing hypotheses for breaking this constraint in sloths have been proposed: (1) the homeosis hypothesis and (2) the primaxial/abaxial repatterning (PAR) hypothesis (Fig. 1). The homeosis hypothesis assumes changes in the *Hox* gene expression pattern that result in the morphological transformation of vertebrae (1, 2, 4, 11, 20). A shorter neck, thus, is associated with homeotic transformation of CV into thoracic vertebrae, whereas a longer neck is the result of homeotic transformation of thoracic vertebrae into CV. Due to pleiotropic effects of mutations in *Hox* genes, homeotic alteration also affects other body parts. However, low metabolic rates in sloths were proposed to result in relaxed selection regimes (1, 4, 14, 21). The PAR hypothesis, in contrast, assumes that the *Hox* gene expression pattern is not altered and the identity of the vertebrae is not changed (5, 6, 12, 22). Accordingly, the number of CV remains the same, but a shift of the abaxial elements (pectoral girdle and limbs) occurred relative to the adjacent and stationary primaxial domain (vertebrae) resulting in shorter and longer necks, respectively. Indeed, the vertebral ossification pattern indicates that the posterior CV in the long-necked sloths (*Bradypus*) are developmentally thoracic (6).

Direct evidence supporting the homeosis hypothesis would involve knowledge of the vertebral *Hox* code for sloths. However, the *Hox* gene expression patterns have been established for actinopterygian fish (23), squamates (24-27), birds (24), crocodilians (28-30), and for the model species mouse (24, 31), but not yet for other mammalian taxa. Consequently, the present study takes advantage of recent works that revealed a correlation between anterior *Hox* gene expression and the quantifiable shape of the CV in the mouse (32) and living archosaurs (crocodile, alligator, and chicken) (29). Following this, changes in the expression of the underlying genetic code can be deduced solely from quantifiable vertebral morphology. Differences in the number of vertebrae with cervical identity would imply a morphological regionalization of the neck that correspond to modifications in *Hox* gene expression domains (expansion of a *Hox* gene's expression domain and/or a shift of gene expression) (29, 30).

Three morphological subunits were detected in the postatlantal cervical vertebral column of the mouse (32). This indicates that two distinct shape changes occur between successive CV (between C2-3 and between C5-6) (32). This morphological modularity detected in the mouse appears to represent the general pattern for living mammals with seven CV (32-34) with overall cervical spine length as the main source of variation in the mammalian neck (35). Since the homeosis hypothesis predicts that the number of vertebrae with cervical identity is changed (1, 4, 11), whereas the PAR hypothesis predicts that the first seven vertebrae retain cervical identity (5, 6, 12), we test the following hypotheses for sloths: (1) The morphological pattern of sloths with seven CV corresponds to the postulated general pattern of living mammals. (2) The morphological pattern of sloths with less than seven CV indicates a decrease in the number of vertebrae with cervical identity. (3) The morphological pattern of sloths with more than seven CV displays an expanded three-subunit pattern indicating an increase in the number of vertebrae with cervical identity. A corroboration of these hypotheses would present evidence for the homeosis hypothesis. This will elucidate the evolutionary mechanism to break the conservatism of cervical count in mammals.

Results

The landmark-based three-dimensional geometric morphometric (3D GM) analysis of the interspecific data set (including all CV of the four specimens together) showed that *Choloepus* and *Bradypus* occupy distinct regions of the morphospace (Fig. S1). *Bradypus variegatus* and *B tridactylus* cluster together, whereas the *C.* cf. *didactylus* 1 and *C. didactylus* 2 do so as well, but show less overlap. In all analyzed sloths, C2 is very distinct in its morphology and is separate from the postaxial vertebrae.

The intraneck data set revealed a distinct morphological differentiation of the neck in all analyzed sloths (Fig. 2A-D). At least 80% of the total variance in the sample is explained by the first two relative warps (RWs) (Table S1) and, thus, the morphospace constructed from RW 1 and RW 2 provides a reasonable approximation of the total shape variation. RW 1 separates C2 from the postaxial vertebrae in each taxon whereas RW 2 separates the postaxial vertebrae into an anterior and a posterior group (Fig. 2). The posterior group comprises the last cervical vertebra in *C.* cf. *didactylus* 1, *C. didactylus* 2, and *B. variegatus*, but the last two CV in *B. tridactylus*.

As confirmed by the cluster analysis (Fig. S2), the RW analysis allowed discrimination of the vertebrae. In all sloths analyzed, the GM analysis revealed a three-subunit pattern (Fig. 2E). The common modular pattern comprises the axis (C2), an anterior and a posterior unit. The distribution of the CV onto the specific modules reveals variation among species. In *C.* cf. *didactylus* 1 (six CV), the modular pattern includes C2, three anterior (C3-5), and one posterior (C6) vertebrae. Including the first thoracic vertebra (V7 in this specimen) in the morphometric analyses confirmed that it is very distinct in its morphology (not shown here). It does not cluster with C6. In *C. didactylus* 2 (seven CV), the morphological subunits comprise C2, four anterior CV (C3-6), and one posterior (C7) cervical vertebra. The morphological subunits of both long-necked sloths (nine CV), *B. variegatus* and *B. tridactylus,* comprised C2, six anterior CV (C3-8) and one posterior (C9) cervical vertebra. Examples of congenital anomalies were found in all specimens (Fig. 3, Fig. S3).

Discussion

Qualitative vs. quantitative morphology

The modular pattern in sloths as quantified by the present morphological analysis is in agreement with the extensive qualitative survey of vertebral morphology of Varela-Lasheras *et al.* (4). The first five or six CV of *Choloepus* and the first eight CV of *Bradypus* have an unambiguous cervical shape (4), which corresponds to the anterior morphological subunit (this study). The last vertebra (C6, 7, and 9, respectively) in the neck always had a transient cervicothoracic shape and rudimentary ribs (4), which corresponds to the posterior morphological subunit (this study). Furthermore, Varela-Lasheras *et al.* (4) observed that the penultimate vertebra in the neck of *Bradypus* (C8) had a transitional cervicothoracic shape in two specimens. Indeed, the modular pattern of *B. variegatus* and *B. tridactylus* differs in the assignment of C8 to the anterior or posterior morphological subunit (Fig. 2C,D). A study of morphological modularity in the vertebral column of modern cats (Felidae) correspondingly revealed a transitional module comprising the last two CV and the first two thoracic vertebrae (C6-T2) (36).

(1) Does the morphological pattern of sloths with seven CV correspond to the postulated general pattern of living mammals?

The morphological three subunit pattern found in the neck of the mouse is viewed as representing the general pattern for living mammals with seven CV (32-34). Two distinct shape changes occur between successive CV: between C2-3 and between C5-6 (32). The present study detected a corresponding modular pattern for *C. didactylus* 2 (seven CV), but the distinct shape change in the posterior part of the neck occurs between C6-7 rather than between C5-6. On basis of the correlation between anterior *Hox* gene expression and quantifiable vertebral shape of the CV in the mouse, this suggests that the expression of *HoxC-5* is shifted posteriorly by one vertebra in *C. didactylus* 2.

Morphological specialization to the suspensory lifestyle of sloths may contribute to the difference in their modular pattern. The CV form a mobile, multi-jointed structure with complex kinematics and requiring the coordination of many muscles (37-39). A reduction of this complexity could be achieved by the regionalization of the cervical vertebral column (33, 40-45). The functionally specialized vertebrae form three compartments and such a reduced geometry was suggested to facilitate moto-neural control of the neck (40, 41). Normally, the cervicothoracic transition involves the last two CV (C6-7), but it appears to be reduced in sloths involving only the last vertebra in the neck. This may again be linked to morpho-functional aspects of their cervical vertebral column. It has been shown in the giraffe that the attachment area of a neck flexor muscle (longus colli) is shifted posteriorly, which was interpreted as providing more flexibility to the neck (46). Suggesting a similar close relationship for the axial musculoskeletal system of sloths, the highly specialized locomotor mode of *Choloepus* is reflected in the intramuscular architecture of their dorsovertebral muscles (47). In terms of shoulder muscles, the development of the serratus ventralis and the rhomboideus may be linked to the posterior subunit in the neck of sloths. Parts of both muscles originate from the posterior CV and insert on the scapula (48, 49). In general, the main function of these muscles is suspension of the thorax between the forelimbs. Due to the inverse body orientation in sloths, however, they are not suited to fulfill this role (48). Correspondingly, these muscles are weakly developed or even absent (13, 48, 50). This may entail that the posterior subunit comprises only the last vertebra instead of two CV as in the mouse.

(2) Does the morphological pattern of sloths with less than seven CV indicate a decrease in the number of vertebrae with a cervical identity?

The modular pattern in the cervical vertebral column of *C.* cf. *didactylus* 1 (six CV) corresponds to the pattern detected in the neck of *C. didactylus* 2 (seven CV), but is shifted by one vertebra since the neck is shorter. The distinct shape change in the posterior part of the cervical vertebral column occurs between the two last vertebrae (C5-6). This suggests for the anterior expression limit of *HoxC-5* to be similar to that of the mouse at C6, but the seventh vertebra is homeotically transformed into a thoracic vertebra in the sloth. More specifically, this indicates that the anterior expression limit of *HoxC-6* is shifted anteriorly by one vertebra in *C.* cf. *didactylus* 1. It has been shown that the expression of the *HoxC-6* gene starts at the first thoracic vertebra in a variety of amniotes that differ in cervical count (24, 27, 30). It corresponds to the transition from cervical to thoracic vertebrae (i.e., cervicothoracic transition) in the mouse (seven CV), chicken (14 CV), goose (17 CV), crocodile (nine CV) and turtle (eight CV) (24, 27, 30).

A similar modular pattern in the cervical vertebral column has been reported for manatees (51). The reduction in cervical count in *Trichechus* from seven to six resembles a homeotic shift and thus further highlights the global validity of the modular pattern of the neck uncovered here (51). However, on basis of the similar relative length of the neck in *Trichechus* (six CV) and *Dugong* (sister-group with seven CV), the reduced manatee cervical count of manatees was not interpreted as a response to selection for a shorter neck, but as global dissociation of the processes of somitogenesis and axial patterning following the PAR hypothesis (51).

(3) Does the morphological pattern of sloths with more than seven CV display an expanded three-subunit pattern indicating an increase in the number of vertebrae with a cervical identity?
The two studied *Bradypus* have more than seven CV, but still displayed a morphological three subunit pattern in the neck corresponding to the general mammalian pattern. This results in a large anterior morphological subunit comprising five and six vertebrae, respectively (Fig. 2E). In correlation with the relative position of the posterior subunit, this indicates a posterior shift of *HoxC-5* expression in the long-necked sloths. The difference in the assignment of C8 to the anterior (in *B. variegatus*) or posterior (in *B. tridactylus*) morphological subunit may suggest either a functional difference or interspecific variation. Since both species do not distinctly differ in behavior and are phylogenetically very close (52, 53), it seems more likely that this part of the neck is subject to interspecific variation.
The last two CV (C8-9) in long-necked sloths are the only vertebrae in the neck whose centra ossify before other cervical centra and neural arches (6). This observation was taken as evidence supporting the PAR hypothesis because the early ossification of C8-9 resembles the anterior-most rib-bearing thoracic vertebrae of other mammals (6). Therefore, the number of vertebrae with a cervical identity was interpreted as unchanged in *Bradypus* and it was inferred that no changes occurred in the *Hox* code (6). Without any further genetic data, it is not possible to exclude this possibility. However, a complex, integrated network of signaling pathways and gene regulators governs bone formation and these molecular mechanisms are not independent of *Hox* gene activity (54). *Hox* genes do not only regulate patterning but also directly influence bone formation and their ossification pattern (54). As an alternative to the argumentation of Hautier *et al.* (6), the difference in ossification of *Bradypus* may therefore be the result of an alteration in *Hox* gene expression. Varela-Lasheras *et al.* (2011) argue that the early ossification of C8-9 does not necessarily suggest the PAR hypothesis because the timing of ossification of vertebral centra and neural arches usually starts somewhere in the thoracic region and proceeds both in anterior and posterior directions (4). It does not identify the position of a specific vertebral region (4).

Cervical ribs and HoxA-5

In contrast to vertebrae, which develop solely from the somitic mesoderm, the ribs derive from both somitic and lateral plate mesoderm (55, 56). Only the distalmost part of the rib (sternal rib) depends on the lateral plate mesoderm and is considered to be an abaxial element (55, 56). The rib head, neck, tubercle, and proximal part of the body derive from the somitic mesoderm and are considered axial elements (55, 56). Following the PAR hypothesis, this suggests a shift between vertebrae including the proximal part of the ribs (primaxial structures) and the distalmost part of the ribs (abaxial structures) (5). Although the present results indicate homeotic transformations of the vertebrae in sloths with aberrant number of CV, the PAR hypothesis cannot be fully rejected in short-necked sloths since the sternal ribs are indeed shifted anteriorly. However, for long-necked sloths, the PAR hypothesis is not supported because the increase in the number of CV is also associated with the loss of cervical ribs.

Several studies reported on the association between the development of cervical ribs and the expression of *HoxA-5* in amniotes (27-30, 32, 57-59). Alligators and crocodiles possess free cervical ribs and the expression limit of *HoxA-5* starts in the posterior cervical vertebral column (28-30). In birds, whose cervical ribs are present, but fused to the vertebrae the anterior expression limit of *HoxA-5* is in the middle region of the neck (28) and *HoxA5* knockdown results in defects of the cervical ribs (60). This contrasts with the more anterior *HoxA-5* expression observed in the mouse (28). The loss of free ribs on the CV (by reduction and fusion) in Mammaliaformes during the Cretaceous (34, 61, 62), suggests that the anterior expression limit of *HoxA-5* is shifted, hence resembling the pattern of the mouse (32). Since the CV in sloths often bear irregular fused riblets, it may be possible that *HoxA-5* expression starts in the posterior region of the neck. It is not likely that a shift of the anterior expression limit of *HoxA-5* occurred twice within one lineage, hence this may indicate so either the lineage towards modern sloths retained a posterior *HoxA-5* expression, or the shift is a side-effect of the change in the expression of other *Hox* genes, in particular *HoxC-5* and *HoxC-6*. Future studies including extinct sloths are required to further elucidate the evolutionary role of *HoxA-5* in axial patterning.

Conclusion

Remarkably, sloths display variation in the number of CV, but a three subunit morphological pattern in the neck is conserved - a pattern that appears to be common for mammals in general. In contrast to archosaurs (cf. Böhmer *et al.*, 2015a, b) (29, 30), the correlation between anterior *Hox* gene expression and quantifiable shape of the CV found in sloths with aberrant cervical count further indicates that the *Hox* code is conserved across living mammals. Our results suggest a mouse-like *Hox* code in the cervical vertebral column of sloths, with an anterior shift of *HoxC-6* expression in association with the first thoracic vertebra in short-necked sloths, and a posterior shift of *HoxC-5* and *HoxC-6* expression in long-necked sloths. In combination with the presence of vertebral anomalies, these observations support the homeosis hypothesis that involves morphological transformation of vertebrae as a result of changes in the *Hox* gene expression pattern. Future analyses on the *Hox* code in non-model organisms, such as sloths, may yield direct evidence for the evolutionary mechanism responsible for the morphological adaptability of the axial skeleton. However, to date, the realization of these analyses is extremely limited. The present study provides a basis for further research including extinct taxa in order to trace the pattern and the underlying genetic mechanisms in the evolution of the vertebral column. Ultimately, this will further our understanding of the processes responsible for the 200-million-year old evolutionary constraint that shapes mammalian evolution (61).

Material and Methods

The present study includes the complete cervical vertebral column of four sloths with variable number of vertebrae in the neck comprising three different species (Table 1).

<u>Quantitative morphological analysis</u>

The morphological variability within the cervical vertebral column is evaluated by geometric morphometrics (GM). A linear regression method for landmark-based GM of vertebrae has been described in Head & Polly (2015) (63), but requires a minimum of at least 10-20 observations for regression analysis (cf. Harrel 2001) (64). Therefore, we here follow the procedure applied by Böhmer *et al.* (2015a) (29) which allows the statistical assessment of shape changes between successive vertebrae in vertebral series comprising less than 10 vertebrae.

Our approach allows the statistical assessment of shape changes between successive vertebrae. A series of 15 homologous landmarks are digitized on the three-dimensional (3D) scans of the CV (C2 to C7) using the software LANDMARK v. 3.0 (65) (Fig. S4). The homologous points capture the vertebral shape in 3D characterizing the morphology of the vertebral centrum and the neural arch. The atlas (first cervical vertebra) is not included in the analysis due to its unique morphology. It lacks specific serial homologies with postatlantal cervicals, and thus, several landmarks thus cannot be applied to it.

Analysis and visualization of the GM data is performed using the software MORPHOLOGIKA (66). Two data sets were analyzed: (1) the interspecific data set includes all CV of the four sloths together and (2) the intraneck data sets include all CV of each taxon separately. The interspecific data set allows evaluating the morphological similarities of the CV across species. The intraneck data sets serve as a basis to identify the morphological modules in each vertebral series. The following procedure was performed on both types of data sets.

Table 1: Specimens analyzed in the present study (ZMB, Museum für Naturkunde Berlin, Germany).

Taxon	#Cervical vertebrae	Collection number
Choloepus cf. *didactylus* 1	6	ZMB_MAM_102634
Choloepus didactylus 2	7	ZMB_MAM_38388
Bradypus variegatus	9	ZMB_MAM_35824
Bradypus tridactylus	9	ZMB_MAM_76147

First, the 3D coordinates of all landmarks were superimposed using a generalized Procrustes superimposition. It removes all the information unrelated to shape (67). Next, a relative warps (RW) analysis was performed to reduce the dimensionality of the dataset and to reveal the similarity relationships among the vertebrae within the cervical vertebral column. The RW analysis constructs a morphospace in which shape variation can be quantified. A cluster analysis using the single linkage algorithm in combination with the Euclidian similarity index was performed on the superimposed landmark coordinates. This joins the CV based on minimal distance between them and results in the quantitative establishment of the morphological subunit pattern in the cervical vertebral column.

Hox gene expression and morphological proxies

The expression of *Hox* genes of the paralogue groups (PG) 3 to 6 are involved in mediating the development of the cervical vertebral column (e.g., 68). In particular, the anterior expression limits of *Hox4* and *Hox5* PG are responsible for the regional patterning in the neck and are the focus of the present study. The somitic *Hox* gene expression pattern in the cervical vertebral column of the mouse was established by a literature survey in Böhmer (32). The survey focused on embryonic stages at which the somites are developed along the full anteroposterior body axis and the somitic *Hox* gene expression limits are thought to be well established and stable during further development (24, 28, 30, 32). Based on the demonstrated correlation between genomic control and phenotypic changes in crocodilians and birds (cf. Böhmer *et al.*, 2015a) (29), the present study of morphological variation of the CV served as a *Hox* gene expression pattern proxy.

Since homeotic transformations induced by mutations of *Hox* genes may be incomplete (e.g., 57, 59, 69, 70) and may result in transitional vertebral identities, the vertebrae were analyzed for the presence of congenital anomalies (such as fusion of vertebrae, left/right asymmetry or rudimentary ribs), following previous studies (4, 5, 71).

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Authors' contributions

CB and JAN conceived and designed the study. EA, PA, AHvH and JAN collected data. CB performed analyses and wrote the manuscript. All authors commented on the manuscript and contributed to its final version.

Additional information

Supplementary information accompanies this paper.

Competing interests

The authors declare no conflict of interest.

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Figures

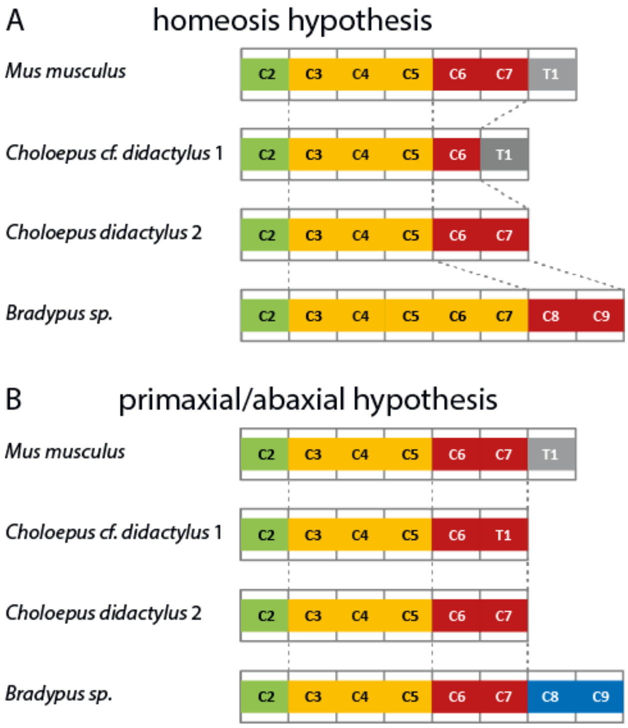

Fig. 1: Two competing evolutionary hypotheses of mechanisms to break the seven cervical vertebrae (CV) constraint in sloths. The *Hox* code is a key determinant of vertebral identity and the color coding indicates in which vertebrae the same *Hox* genes are expressed. A three subunit pattern within the postatlantal CV has been found (green, axis; yellow, anterior; red, posterior). Thoracic vertebrae shown in grey. A: The homeosis hypothesis predicts that the number of CV is changed due to an altered *Hox* code. Therefore, the modular pattern in the neck of sloths with an aberrant number of CV should differ from that of living mammals (represented by the mouse), e.g., due to expansion of one of the subunits. B: The primaxial/abaxial repatterning (PAR) hypothesis predicts that the first seven vertebrae retain a cervical identity and the *Hox* code remains unchanged. According to the PAR hypothesis the modular pattern in sloths corresponds to the general pattern of living mammals and CV that are originally thoracic vertebrae are added (blue).

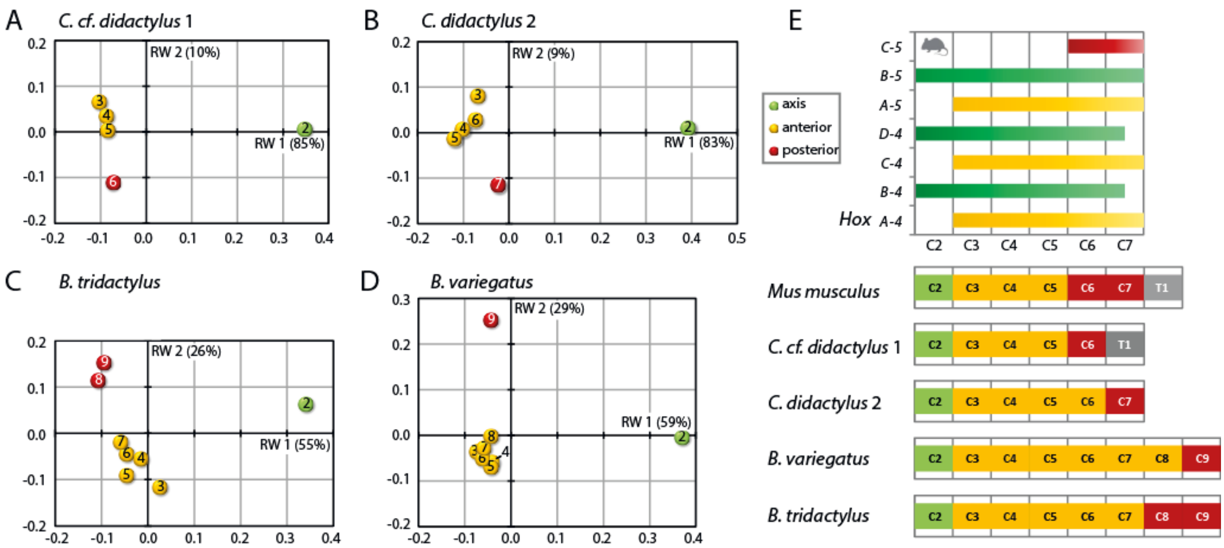

Fig. 2: Relative warps (RW) analysis results of the intraneck dataset. The plots show the shape differences within the cervical vertebral column along RW 1 and RW 2 for each specimen (A-D). The morphological analysis allowed discrimination of the vertebrae in three different subunits (indicated by color coding) (E). The correlation between somitic *Hox* gene expression pattern and morphological modularity in the neck of the mouse (*Mus musculus*) is based on Böhmer et al. (2015b) (30) and Böhmer (2017) (32). Corresponding to the mouse, two distinct shape changes are revealed between successive CV in all analyzed sloths. The modular pattern in the neck of sloths with additional CV differs in displaying an expanded anterior region of the neck (yellow).

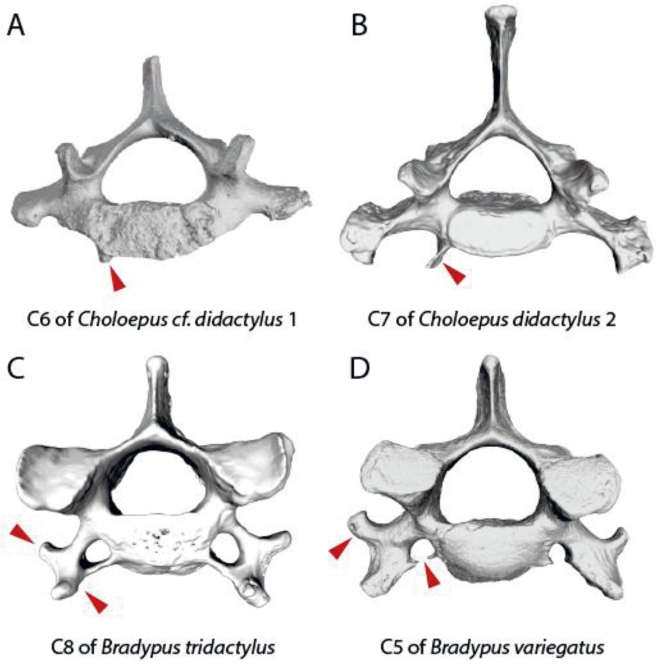

Fig. 3: Congenital anomalies were found in all analysed sloth specimens. Anterior view of different, 3D rendered CV with red arrow heads pointing to malformations. A, the last cervical vertebra (C6) of *C.* cf. *didactylus* 1 displays unilaterally a ventral process. B, the last cervical vertebra (C7) of *C. didactylus* 2 shows unilaterally a ventral process. C, lateral transverse processes of C7 and C8 in *B. tridactylus* are not developed symmetrically (C8 shown here). D, on the C5 in *B. variegatus* the foramina transversaria of are not entirely closed and transverse processes are not developed symmetrically.

Chapter 5

Synopsis

The evolutionary morphology of the mammalian neck

The constancy of seven cervical vertebrae across mammals is one of the most conspicuous examples of morphological stasis in vertebrate evolution. Interspecific variability of the neck is nevertheless present and disparity is considerably high. The aim of this dissertation was two-fold. First, the disparity of the neck was quantified and compared across mammals. Second, the obtained invariable and conserved traits of the neck were discussed in the context of developmental constraints, biomechanical determinants and phylogenetic history. The fundamental developmental processes governing the limited number of vertebrae (Chapter 1, Galis and Metz 2003; Buchholtz et al. 2012) and the resulting shape differences among the cervical vertebrae (Johnson et al. 1999; Buchholtz et al. 2012; Arnold et al. 2016) have extensively been examined. Hence, the focus of the dissertation was placed on allometry of the cervical spine, the musculoskeletal organization of the neck, and the modularity of the cervical Hox gene anterior-posterior pattern.

Methodology

Three different methods were used to assess the evolutionary morphology of the mammalian neck. In general, these methods are quite different and aim to capture different aspects of neck morphology.

Traditional linear morphometrics were applied to the cervical spine as a whole and for the individual vertebrae by measuring absolute and relative vertebral body length in Chapter 2. Vertebral centrum length has been shown to be the major morphological change of vertebrae along the cervical series as well as across the cervical spine of different species of different size

(Johnson et al. 1999; Breit and Künzel 2004; Badlangana et al. 2009; Arnold et al. 2016; Randau et al. 2016). Using a rather simple metric facilitated the comparison of the cervical vertebrae among each other despite some of them lacking specific features or having unique morphology (e.g., unique morphology of atlas and axis, the ventral lamina of C6, missing transverse foramina and ventral tubercles of transverse processes in C7; see Arnold et al. 2016; Randau et al. 2016) and in a phylogenetical large sample. It further enabled the calculation of intracervical proportions. Intersegmental proportions have been shown to provide crucial insight into functional morphology of the mammalian limb without explicit knowledge of shape difference related to ecology or locomotor mode (e.g., Elissamburu and Vizcaíno 2004; Schmidt 2005; Schmidt and Fischer 2009). They allow the inference of basic biomechanical properties governing the whole structure (for limb, cf. Seyfarth et al. 2001)). For this reason, intracervical proportions were analyzed in detail for the first time and provide insights in the conserved intracervical organization across mammals (Chapter 2).

As the head-neck motor system not only consists of the cervical vertebrae but also of a high number of muscles, both osteological and myological data were integrated into the analyses in Chapter 3. Muscles (or their mesoderm precursor cells) emigrating from the neck during embryonic development have been analyzed in detail due to their crucial role in structuring the mammalian trunk (Buchholtz 2012; Hirasawa and Kuratani 2013). The limb muscles that have expanded into the neck region during mammalian evolution, however, have not been examined in terms of their impact on neck organization. Although a few studies compared the neck muscle arrangement interspecifically in an evolutionary context (e.g., Bekele 1983; Filan 1990; Diogo 2009; Diogo and Wood 2011), the comparison was only qualitatively due to the high number and complex arrangement of muscles. This prevented any quantification of the differentiation of the neck muscle arrangement. It remains unknown whether the interspecific variation in muscle attachments actually results in changes in the overall musculoskeletal organization of the neck across mammals. Due to its high complexity and topological heterogeneity, neck muscle arrangement could be described using network theory. Networks are a common tool in biological science for analyzing and visualizing complex systems and their interactions (e. g., Watts and Strogatz 1998; Williams and Martinez 2000; Sole and Montoya 2001; Dunne et al. 2002; Girvan and Newman 2002; Alon 2003; Romanuk et al. 2009). Recently, tools were developed allowing the analyses of the organization of bony structures like the tetrapod skull (Esteve-Altava et al. 2011; Esteve-Altava et al. 2013). This was further extended to include not only bones, but also muscles within the same network analysis (Esteve-Altava et al. 2015; Dos Santos et al. 2017; Molnar et al. 2017). Using the recent advancements in the field, the novel and state-of-the-art approach of anatomical network analysis (AnNA) has been applied to the mammalian neck. AnNA offers a mathematical description of the organization of a certain structure by formalizing bones, muscles, and their physical interactions into the nodes and links of a network (Rasskin-Gutman and Esteve-Altava 2014). In this way, AnNA is comparable with modern geometric morphometrics as both translate complex biological information into mathematics. However, the mathematics behind the translation highly differs between the approaches, as they aim to capture a different kind of biological information (anatomical organization *versus* morphological variation; see Esteve-Altava 2017 for a detailed discussion of the methodological and theoretical differences).

The study in chapter 4 took advantage of recent studies that revealed a correlation between anterior gene expression and the quantifiable shape of the cervical vertebrae in mice (Böhmer 2017) and living archosaurs (crocodile, alligator, and chicken; Böhmer et al. 2015). Following these studies, changes in the expression of the underlying genetic code can be deduced solely from quantifiable vertebral morphology. Differences in the number of vertebrae with cervical identity implied either a morphological regionalization of the neck that correspond to modifications in Hox gene expression domains (expansion of a Hox gene's expression domain and/or a shift of gene expression) or an integration of true thoracic vertebrae in the neck in *Bradypus* and an integration of cervical vertebrae into the trunk in *Choloepus*, respectively (Böhmer et al. 2015; Böhmer 2017).

Regionalization and modularity of the mammalian neck

The analyses of vertebral allometry, musculoskeletal organization and Hox gene modularity in this dissertation allow new insights in the regionalization or modularity of the mammalian neck, and its comprehensive interpretation in regard to the developmental constraints 'fixing' the number of cervical vertebrae.

Several studies suggest a more or less significant regionalization of the mammalian neck (Table 1). The list was complemented and extended by the observations from Chapter 2 to 4, revealing a partition on additional morphological aspects that were unnoted to date. Interpreted altogether, the different modes of regionalization of the neck proposed in the chapters of this dissertation and in former studies 'act' on different levels of morphological integration.

Table 1 Regionalization and modularity of the mammalian neck on different levels of integration

Level of integration	**Trait**	**Regionalization**	**References**
structural	Shape variation among cervical vertebrae	 C1 C7	Johnson et al. 1999; Buchholtz et al. 2012; Arnold et al. 2016; Randau et al. 2017
	Shape allometry		Randau et al. 2016
	Vertebral centrum length allometry and proportions		Chapter 2 (Arnold et al. 2017)
	Musculoskeletal organization		Chapter 3
developmental	Relationship between cervical vertebral shape and Hox gene pattern (mouse model)		Böhmer 2017
	Relationship between cervical vertebral shape and Hox gene pattern (sloths)	 *Bradypus*  *Choloepus*	Chapter 4
	Cervical mesoderm patterning/migratory muscle precursor cell streams		Buchholtz et al. 2012
functional	Resting posture of the neck		Vidal et al. 1986
	Movements and kinematics of the neck		Graf et al. 1995a; Graf et al. 1995b

The *structural* regionalization mainly is based on the characteristic shape variation among the vertebrae within the cervical spine. There are distinct shape changes between C2 and C3 as well as C5 and C6 (Table 1). The atlas and axis, but also C6 and C7, each have unique morphologies, whereas C3 to C5 are more uniform (Evans 1939; Johnson et al. 1999; Buchholtz et al. 2012; Arnold et al. 2016; Böhmer 2017; Randau et al. 2017). Although the cervical vertebrae show secondary adaptations to ecology and locomotor mode (Osburn 1903; Shimer 1903; Lull 1904), this basic morphological pattern among them is conserved across species and was not even altered during domestication (see references above). The impact of body size on the morphology and regionalization of the cervical spine, in contrast, is much more complex. Although altering body size is a crucial component of mammalian evolutionary diversification, the associated biomechanical implications raise an important evolutionary challenge (Thompson 1917; Huxley 1932). As size and locomotor related changes in vertebral shape and proportions are usually attributed to the (thoraco)lumbar spine (e.g., Jones 2015a; Jones 2015b; Jones and Pierce 2016), allometric analyses of the cervical region are rare in the literature. Randau et al. (2016) recently presented the most extensive systematic examination including all seven neck vertebrae. They uncovered the shapes of C4 and C5 having uniform scaling properties across species, whereas the more anterior and posterior vertebrae scale individually (Table 1). As this study was limited to felids however (which have relatively uniform body proportions), the allometric analysis of vertebral lengths and proportions was extended to mammals in general in Chapter 2 (Arnold et al. 2017). The primary bivariate analyses revealed differences in the scaling properties between C1 and the rest of the cervical vertebrae (C2-C7). C1 length increases with increasing body size and accounts for increasing head load (Chapter 2). In contrast, C2 to C7 decrease with increasing body size and account for increasing distance between the head and trunk. Thus, allometric response of the vertebral lengths and proportions suggested ‘only’ a bipartite regionalization. Subsequent multivariate analysis uncovered subtle differences between C2+C7 and C3-C6 (Chapter 2). Vertebral proportions are quite uniform across the majority of mammalian species and in this aspect resemble to some degree mammalian hind limb proportions (Schmidt and Fischer 2009). Under specific loading conditions on the cervical spine (big heads and head appendages, aquatic and fossorial lifestyle, elongated necks), however, the general pattern is altered by increasing the proportion of one of the three regions (C1, C2+C7, or C3-C6, respectively) (Chapter 2).

The structural regionalization uncovered in the shape and allometry of the cervical vertebrae has also been revealed for the cervical musculature in Chapter 3. It was the first study that examined the muscles of the neck with respect to the meristic constraints and modularity of the cervical spine. Although several network parameters (e.g., morphological complexity) and the arrangement of pectoral muscles are variable, a tripartite axial regionalization is highly conserved across mammalian species (Table 1, Chapter 3). The three musculoskeletal regions are not completely consistent with those suggested by vertebral shape changes (Johnson et al. 1999; Buchholtz et al. 2012; Arnold et al. 2016; Randau et al. 2017). These regions, defined by vertebral shape, represent morphological specializations to the junction between the cervical and thoracic spine, as well as the cervical spine and the head. The muscles, however, bridge these junctions in order to induce basic movements of the neck (Vidal et al. 1986). For this reason, regional boundaries defined by musculoskeletal organization in Chapter 3 (C1/C2 and C4/C5) are shifted anteriorly compared those defined by vertebral shape (C2/C3 and C5/C6) (Table 1).

The *developmental* regionalization has recently been shown by the close relationship of vertebral shape and the underlying Hox gene anterior-posterior pattern (Böhmer 2017). The relationship was uncovered for the mouse model and suggests a close correspondence between cervical regions defined by vertebral shape and those defined by the Hox genes (Table 1). Due to the conserved sequence of cervical vertebral shapes descending the neck, this Hox gene based regionalization most likely represents the general pattern for mammals and even therapsids (Böhmer 2017). To test for the global validity of this regionalization, the same approach was applied to extant tree sloth in Chapter 4, as they represent one of the rare deviations from the mammalian 'rule of seven' cervical vertebrae (Owen 1853, 1866; Bateson 1894; Buchholtz and Stepien 2009; Varela-Lasheras et al. 2011). Although the number of cervical vertebrae in *Choloepus* and *Bradypus* is decreased and increased, respectively, the underlying Hox gene modularity is not changed (Chapter 4). The sequence of vertebral shapes typical for mammals with usual cervical count (including three morphological modules), however, is condensed to six or stretched to nine vertebrae, respectively (Chapter 4). This suggests that the meristic constraint may be broken in sloths (Buchholtz and Stepien 2009; Buchholtz 2012), but developmental modularity is maintained (see also (Buchholtz et al. 2014).

Modular suites of Hox genes not only give rise to modularity in cervical vertebral shape but are also proposed to facilitate modularity in cervical mesoderm (Buchholtz et al. 2012). The origin of streams of migratory muscle precursor cells divide the neck into an upper (forming the head/neck articulation), a medial (somatic origin of the diaphragm muscles and the phrenic nerve), and a lower region (cervico-thoracic transition, somatic origin of the forelimb muscles and the brachial plexus; Buchholtz et al. 2012) during development (Table 1).

Finally, mammalian necks are also *functionally* regionalized. Although functional regionalization was not part of the focus of the thesis, it should be briefly reviewed here to give a thorough overview on modes of regionalization in the mammalian neck. Mammals adopt a stereotypical resting posture with the head closely retracted to the trunk (Vidal et al. 1986; Vidal et al. 1988). To reduce the distance between the weight of the head and the sustaining cervico-thoracic junction, the cervical spine is held as vertically as possible. Due to this s-shaped and self-stabilizing posture, changes in gaze are restricted to movements in the cranio-cervical (Occiput-C1-C2) and cervico-thoracic junction (C6-C7-Th1) in the sagittal plane (Graf et al. 1995b). The mid-cervical region does not contribute to sagittal motion but is rather involved in axial rotation. This functional tripartition (Table 1) results in parallelogram-like movements of the head in terrestrial mammals (Graf et al. 1995a). It further accounts for a reduction of the degrees of freedom in a kinematic multi-body chain (Bernstein 1947; Bizzi et al. 1976; Peterson et al. 1989; Pellionisz et al. 1991; Bout 1997) that have to be coordinated by autonomous neural control.

Evolutionary trait-off between meristic constraints and functional diversity

Most of the proposed modes of regionalization discussed above are very similar in dividing the neck into an upper (C1, C2), middle (C2-C5), and lower (C6, C7) compartment. The allometry of the vertebral shapes (Randau et al. 2016) and proportions (Chapter 2) and the musculoskeletal organization (Chapter 3), however, suggest alternative divisions of the neck (Table 1). Nevertheless, all modes of regionalization have in common that derived or specialized traits always occur on both ends of the neck. C1 facilitates the head-neck transition and compensates the differences in developmental origin, allometry, and cross-sectional area between the occiput and axial spine. In contrast, C7 (or the last vertebra with cervical identity in sloths) facilitates the neck-trunk transition and the break in axial mobility (rib-bearing *versus* non-rib-bearing axial series). This is promoted by the increased mobility of C6 and its derived morphology of the ventral tubercle of the transverse process (rib rudiment, Chassaignac tubercle; Slijper 1946; Graf et al. 1995a; Arnold et al. 2016). C2 is intermediated between the upper and middle cervical region. On the one hand, it is developmentally and functionally part of the head joint (Evans 1939; Jenkins 1969). On the other hand, it provides the transition between the specialized head joint and the ‘ordinary’ vertebrae by its allometric properties and the insertions of axial musculature (Chapter 2 & 3). Conserved multi-level regionalization or modularity is combined with the strong meristic constraints in neck of mammals.

The morphological regionalization (structural, functional) is thought to be the product of the secondary developmental regionalization of originally overlapping Hox expression domains (Pollock et al. 1995; Wellik 2007), and is classically associated with developmental and evolutionary constraints, specifically the restriction of count (Raff 1996; Buchholtz 2012). This close association between morphological modularity and developmental constraints has extensively been discussed by Kuratani (2009). The morphological-developmental modules provide the cue to the 'stiffness' and 'softness' in evolutionary change of the mammalian neck (Kuratani 2009). On the one hand, the conserved modular patterns in terms of vertebral shape, allometry, musculoskeletal organization, or mesoderm patterning in the neck (Chapter 2-4, Johnson et al. 1999; Buchholtz 2012; Arnold et al. 2016; Randau et al. 2016; Randau et al. 2017) are related to the expression of conservative genes, namely the anterior-posterior Hox gene cascade (Johnson and O'Higgins 1996; Galis 1999; Buchholtz 2012; Woltering and Duboule 2015; Böhmer 2017). The close relationship between the morphological and developmental regionalization has been particularly highlighted in chapter 4 for the extant tree sloths, which broke the mammalian 'rule of seven' but not the neck modularity itself. As this conservation serves as developmental constraints that maintain morphological modules, it becomes hard to override by (directional) selection (Wagner 1989; Kuratani 2009).

On the other hand, the developmental and morphological modularity allows for regional specialization through the autonomy of the modules (Kuratani 2009). The highly derived atlas-axis complex might be the best example here. The three neck regions (upper, middle, lower) differ in many cervical traits (summarized in Table 1 and the references therein) but the differences are generally similar across species. Body size and prey capture behavior seem to affect this regional differentiation to a minor extent only (Arnold et al. 2014, Randau et al. 2016, Chapter 2 & 3). Thus, regionalization mainly serves for an increased mobility of a kinematic chain with a limited number of elements in general (which can be tracked in the fossil record; see introduction). This in turn accounts for the high functional diversity of the neck in mammals. The neck functions as the manipulator of the head and houses the sensory apparatus of hearing, vision, smell, and taste, and the center of motor control (Bogduk and Mercer 2000). Accordingly, the neck has a leading biological role during many activities like exploration, orientation, foraging, drinking, gaze stabilization during locomotion, grooming, social display etc. (Van Der Leeuw et al. 2001). Thus, it has to meet a wide variety of functional demands in terms of different head trajectories during many behaviors (Zweers et al. 1994; Van Der Leeuw et al. 2001). Accordingly, the strongly conserved modularity and regionalization in the mammalian neck represents an evolutionary trade-off between the meristic constraints and functional diversity (also see Böhmer 2017).

The constraints and the trade-off, however, do not minimize or prevent disparity in the neck across mammalian lineages. Disparity is albeit realized in cervical traits not directly related to modularity. For instance, variation in cervical spine length as a whole is a major source of disparity in the neck, whereas intracervical proportions are uniform across the majority of species (Chapter 2). Furthermore, the pectoral muscles provide disparity in the musculoskeletal organization of the neck by contributing to different modules whereas axial musculature is uniformly regionalized (Chapter 3). Finally, even the meristic constraints are broken and the number of cervical vertebrae is change in sloths and manatees (Buchholtz and Stepien 2009; Varela-Lasheras et al. 2011; Buchholtz et al. 2014) but the underlying modularity is still valid (Chapter 4).

Conclusion and Outlook

This thesis aims to enhance the knowledge on the disparity and constraints of the mammalian neck. The general morphology of the mammalian neck is channeled by strong developmental constraints and biomechanical determinants. The deep-time conservation of seven cervical vertebrae distinctly predated the origin of the mammalian lineage and is unrelated to the actual function of the neck as head actuator. It was suggested in recent studies that the neck in mammals might be regionalized based on several cervical traits. Further modes of regionalization are uncovered here for vertebral scaling and proportions, musculoskeletal organization, and the Hox gene anterior-posterior pattern in sloths (Chapters 2-4). Discussed together, they represent a regionalization or modularity on different levels of integration (i.e., structural, developmental, and functional; see Table 1). This multi-level modularity results from the strong developmental constraints on cervical number and the expression of the highly conserved Hox genes, but otherwise promotes regional specialization accounting for the variety of functional demands on the neck in mammals (Kuratani 2009; Böhmer 2017). Disparity in the neck nevertheless emerges either by global system variation (variation in neck length as a whole, increase/decrease in cervical number) or the integration with the forelimb.

Based on these findings, future research on the evolution of the mammalian neck is proposed to go in three directions. First, it should focus on two lineages shown to have the most disparate necks (Chapter 2 &3). Cetartiodactyls not only cover a huge range of body sizes but also the extremes in neck lengths (giraffes *versus* whales), locomotor modes (cursorial *versus* aquatic), and head appendages (horns and antlers). Xenarthrans on the other hand, although relatively scarce in species, show remarkable adaptations of the neck to different ecologies in all three lineages (i.e., armadillos, anteater, and sloths). The breaking of the meristic constraints in sloths can only be fully understood if the three lineages are examined together and with the inclusion of fossil forms. Second, more field and laboratory studies are needed that quantify the motions and usage of the neck across species in order to understand the impact of the meristic constraints and regionalization on neck mechanics. This is, to date, limited to the few model animals in the studies of Graf et al. (1995a; 1995b) as well as to horses (reviewed in Zsoldos and Licka 2015). Third, special emphasis should be placed on fossils near the historical fixation of the mammalian 'rule of seven' cervical vertebrae. As well preserved specimens exist, for instance of *Thrinaxodon* (Fernandez et al. 2013), functional and mechanical analysis would possibly provide insights in the emergence of the regionalization that followed the meristic fixation.

Summary

The constancy of seven cervical vertebrae in the neck of almost all mammals is one of the most outstanding examples of morphological stasis in vertebrae evolution. Pleiotropic effects of underlying Hox genes and a mammal specific cervical mesoderm patterning result in strong developmental constraints that prevent meristic variability in the neck. The fixation of cervical count dates back more than 200 million years and was followed by specific modifications of vertebral morphology (e.g., reduction and fusion of cervical ribs, consolidation of the atlas-axis-complex). As the biomechanics of head and neck suspension further determines overall neck morphology, it is yet unclear how morphological disparity is manifested in the neck of mammals in accordance to variation in body size, ecology, ad head use. This dissertation aims to contribute to the understanding of the evolutionary morphology of the mammalian neck. The scope of the thesis is on the question which cervical traits (despite the fixed number) are further constrained and how disparity emerges. Finally, the role of the regionalization or modularization of the neck is examined and discussed.

The dissertation comprises of five chapters. The general introduction is followed by three chapters that are each written to stand on their own and to be published in peer-reviewed journals. These three chapters consider different aspects of the evolutionary morphology of the mammalian neck. The last chapter discusses the insights gained from the individual analyses in the context of neck regionalization.

Different approaches are applied to analyze different aspects of neck morphology and regionalization. Linear metrics of the cervical spine as a whole and of the individual cervical vertebrae as well as the vertebral proportions are analyzed with phylogentic comparatives methods. The in-depth analysis of the allometry across a large sample of mammalian species is used to reveal which role body size and neck length play in neck disparity. The musculoskeletal organization of the neck is analyzed within the novel, state-of-the-art framework of anatomical network analysis. Neck organization and modularity are characterized by seven network parameters and interpreted in their morphological context. The evolution of neck organization before and after the Cretaceous–Tertiary boundary is evaluated using a disparity-through-time analysis.

Finally, the cervical Hox gene pattern in extant tree sloths is inferred from the shape differences among their cervical vertebrae. As sloths represent a conspicuous deviation from the mammalian 'rule of seven' cervical vertebrae, their Hox gene pattern provides insides in the developmental background of the evolutionary variability in the mammalian neck.

The allometric analysis reveal that the modification of the cervical spine lengths as a whole is a major source of variability of mammalian necks. Opposite allometric scaling of C1 and C2-C7 accommodates the increase of head weight and neck bending moment with body size, respectively. Vertebral proportions are uniform across the majority of mammalian species. Under extreme loading conditions on the cervical spine (big heads and head appendages, aquatic and fossorial lifestyle, elongated necks), however, the general pattern is altered by increasing the proportion of one of the three regions (C1, C2+C7, or C3-C6, respectively). The anatomical network analysis shows that mammalian necks are characterized by a combination of conserved and highly variable network properties. This is related to a conserved regionalization of the musculoskeletal organization of the neck into upper, mid and lower cervical modules as well as a varying degree of specialization and integration of the pectoral elements. Additionally, there are striking differences in the organization of the neck between monotreme and therian mammals. Higher disparity in neck morphology, however, evolved late in mammalian history, particularly in parallel with the radiation of certain lineages (e.g., cetartiodactyls, xenarthrans). The shape changes among the cervical vertebrae of extant tree sloths uncover a conserved Hox gene pattern and modularity in mammals. Although the number of cervical vertebrae in *Choloepus* and *Bradypus* is decreased and increased, respectively, the underlying Hox gene modularity (i.e., an anterior, medial, and posterior module) is not changed. The sequence of vertebral shapes typical for mammals with usual cervical count, however, is condensed to six or stretched to nine vertebrae, respectively.

Different modes of regionalization of the mammalian neck were suggested in earlier studies and this concept is extended in this thesis. Altogether, they represent a regionalization or modularity on different levels of integration (i.e., structural, developmental, and functional). This multi-level modularity results from the strong developmental constraints on cervical number and the expression of the highly conserved Hox genes but otherwise promotes regional specialization accounting for the variety of functional demands on the neck in mammals. The morphological-developmental modules provide the cue to the 'stiffness' and 'softness' in evolutionary change of the mammalian neck. On the one hand, the conserved modular patterns in terms of allometry, musculoskeletal organization, or vertebral shape mesoderm pattening in the neck are related to the expression of conservative gene modules, namely the anterior-posterior Hox gene cascade. As this conservation serves as developmental constraints that maintain morphological modules, it becomes hard to override by (directional) selection. On the other hand, the developmental and morphological modularity allows for regional specialization through the autonomy of the modules. The constraints and the trade-off, however, do not minimize or prevent disparity in the neck across mammalian lineages. Disparity is albeit realized in cervical traits not directly related to modularity (e.g., modification of neck length, varying integration of pectoral muscles, variation in vertebral number).

Zusammenfassung

Die Konstanz von sieben Halswirbeln in fast allen Säugetieren stellt eines der bemerkenswertesten Beispiele morphologischer Stasis in der Evolution der Wirbeltiere dar. Meristische Variabilität wird dabei durch starke entwicklungsbiologische Einschränkungen unterbunden. Diese entstehen durch pleiotrope Effekte der zugrundeliegenden Hox-Gene und eine säugetier-spezifische Musterbildung des Halsmesoderms. Die Fixierung der Halswirbelzahl reicht über 200 Millionen Jahre zurück und resultierte in spezifischen Modifikationen der Wirbelmorphologien (z.B. die Reduktion und Fusion der zervikalen Rippen und die Konsolidierung des Atlas-Axis-Komplexes). Da die Morphologie des Halses zudem stark von der Biomechanik der Kopf- und Halsaufhängung bedingt ist, ist es bisher noch unklar, wie sich morphologische Diversität aufgrund der Variation der Körpergröße, Ökologie und Kopfbewegungen im Hals der Säugetiere manifestiert. Die vorliegende Dissertation hat zum Ziel, das Wissen um die evolutionäre Morphologie des Säugetierhalses zu erweitern. Im Fokus steht hierbei die Frage, welche zervikalen Merkmale (mit Ausnahme der Wirbelanzahl) in ihrer Variation eingeschränkt sind und wie morphologische Diversität trotz allem entsteht. Abschließend wird die Rolle der Regionalisierung und Modularisierung des Halses untersucht und diskutiert.

Die Dissertationsschrift besteht aus fünf Kapiteln. Nach einer allgemeinen Einleitung folgen drei Kapitel, die als alleinstehende Manuskripte in Fachzeitschriften publiziert bzw. bei diesen eingereicht wurden Jedes der drei Kapitel beleuchtet einen anderen Aspekt der evolutionären Morphologie des Hales der Säugetiere. Im letzten Kapitel werden die Erkenntnisse der Einzelanalysen im Kontext der Regionalisierung des Halses diskutiert.

Die verschiedenen Aspekte der Halsmorphologie und –regionalisierung werden in den einzelnen Kapiteln durch unterschiedliche Methoden beleuchtet.
Die Halswirbelsäulenlänge, die individuellen Wirbellängen und die Wirbelproportionen werden mittels vergleichend-phylogenetischer Methoden analysiert. Der Einfluss der Körpergröße und Halslänge auf die morphologische Diversität des Halses wird durch eine detaillierte Allometrieanalyse von mehr als 350 Säugetierarten aufgezeigt. Durch die neuartige Methode der anatomischen Netzwerke kann die muskuloskeletale Organisation der Hälse verschiedener Säugetierarten vergleichend untersucht werden. Die Organisation und

Modularität des Halses wird dabei durch sieben Netzwerkparameter charakterisiert, welche anschließend morphologisch interpretiert werden. Zusätzlich wird die Evolution der Halsorganisation vor und nach der Kreide-Tertiär-Grenze verglichen. Abschließend wird das Hox-Gen-Muster der rezenten Faultiere von den Gestaltänderungen der Halswirbel abgeleitet. Da Faultiere bemerkenswerte Abweichungen von der ‚Regel der sieben Halswirbel' bei Säugetieren aufweisen, erhält man durch ihr Hox-Gen-Muster Einblicke in den entwicklungsbiologischen Hintergrund der evolutionären Variabilität des Säugerhalses.

Durch die allometrischen Analyse in Kapitel 2 wird deutlich, dass die Modifikation der Halswirbelsäulenlänge bedeutend zur Variabilität des Halses beiträgt. Die gegensätzliche Skalierung von C1 und C2-C7 bei zunehmender Körpergröße gleicht dabei sowohl das steigende Kopfgewicht als auch das steigende Drehmoment im Hals aus. Die Wirbelproportionen sind jedoch beim Großteil der untersuchten Arten einheitlich. Nur unter extremen Belastungen des Halses (z.B. große Köpfe und Kopfanhänge, aquatische und grabende Lebensweise, verlängerter Hals) sind die Proportionen einzelner Wirbelregionen (C1, C2+C7 oder C3-C6) erhöht.
In Kapitel 3 zeigen die Analysen der anatomischen Netzwerke auf, dass die Hälse der Säugetiere durch eine Kombination aus konservativen und variablen Merkmalen gekennzeichnet sind. Dies ist durch die konservative Regionalisierung des Hales in ein oberes, mittleres und unteres Modul, den variierenden Grad der Spezialisierung des Halses und die Integration der Pectoralelemente bedingt. Zusätzlich können bedeutende Unterschiede zwischen den Monotremen und den Theria gezeigt werden. Eine erhöhte morphologische Diversität evolvierte jedoch vergleichsweise spät und parallel zur Radiation bestimmter Gruppen (z.B. Cetartiodactyla, Xenarthra).
Die in Kapitel 4 untersuchten Gestaltsunterschiede der Halswirbel der Faultiere lassen auf ein konservatives Muster bzw. eine konservative Modularisierung der Hox-Gene in der Halsregion der Säugetiere schließen. Obwohl die Halswirbelzahl in *Choloepus* reduziert bzw. in *Bradypus* erhöht ist, ist die Hox-Gen-Modularität unverändert (ein vorderes, mittleres und hinteres Modul). Die Abfolge der positionsspezifischen Gestalt der einzelnen Wirbel ist jedoch im Vergleich zu Säugetier mit sieben Halswirbeln auf sechs gestaucht bzw. auf neun gestreckt.
Verschiedene Modi der Regionalisierung des Säugetierhalses waren bereits Gegenstand früherer Studien. Dieses Konzept wird durch die Ergebnisse der vorliegenden Dissertation erweitert.

Insgesamt ist das System Hals durch Regionalisierung oder Modularität auf verschiedenen Integrationsebenen (strukturell, entwicklungsbiologisch und funktionell) charakterisiert. Diese Multi-Level-Modularität resultiert aus den starken entwicklungsbiologischen Beschränkungen und der Expression konservativer Hox-Gene. Sie begünstigt jedoch auch die regionale Spezialisierung, um eine Fülle von funktionalen Ansprüchen an den Hals zu gewährleisten. Die morphologisch-entwicklungsbiologischen Module sind dabei nicht nur der Schlüssel zum evolutionären Konservatismus sondern auch zur evolutionären Variabilität. Auf der einen Seite basiert die konservative Modularität der Wirbelgestalt, Allometrie, muskuloskeletalen Organisation und Mesoderm-Musterbildung auf der Expression der modularen Hox-Gene. Da dieser Konservatismus als entwicklungsbiologische Einschränkung auf den Erhalt der Module wirkt, ist er nur schwer durch (gerichtete) Selektion außer Kraft zu setzten. Auf der anderen Seite erlaubt die entwicklungsbiologische und morphologische Modularität ein hohes Maß an regionaler Spezialisierung durch die Autonomie der Module. Dieser Zielkonflikt und die Beschränkungen verhindern oder minimieren jedoch nicht die morphologische Diversität des Halses in den verschiedenen Linien der Säugetiere. Die morphologische Diversität realisiert sich allerdings zumeist in zervikalen Merkmalen, die nicht in direktem Zusammenhang mit der Regionalisierung stehen (z.B. Modifikation der Halslänge, variierende Integration der Pectoralmuskeln, Variation der Halswirbelzahl).

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Declaration

Ehrenwörtliche Erklärung

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbständig und nur unter Verwendung der angegeben Hilfsmittel und Literatur verfasst habe. Es wurden keine Textabschnitte eines Dritten oder eigener Prüfungsarbeiten ohne Kennzeichnung übernommen. An der Erstellung der in der vorliegenden Arbeit verwendeten Originalarbeiten und Manuskripte haben Co-Autoren mitgewirkt. Mein Eigenanteil ist in der Arbeit ausgewiesen. Die Hilfe eines Promotionsberaters wurde nicht in Anspruch genommen. Dritte haben weder unmittelbar noch mittelbar geldwerte Leistungen für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen. Die Promotionsordnung der Biologisch-Pharmazeutischen Fakultät der Friedrich-Schiller-Universität Jena ist mir bekannt.

Ich erkläre, dass ich mich mit der vorliegenden Arbeit an keiner anderen Hochschule um einen akademischen Grad beziehungsweise um eine staatliche oder andere wissenschaftliche Prüfung beworben habe. Ich habe weder früher noch gegenwärtig die Eröffnung eines Verfahrens zum Erwerb des Grades Dr. rer. nat. an einer anderen Hochschule beantragt.

Jena, 09.04.2018 Patrick Arnold

Appendix

Supplementary Material of Chapter 2

Differential scaling patterns of vertebrae and the evolution of neck length in mammals

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Supplementary information on timetree construction

The Timetree of Life (TOL) resolved at the species level (accessed at http://timetreebeta.igem.temple.edu/ (Hedges et al. 2015) was modified with Mesquite 3.10 (Maddison and Maddison 2011). All taxa that were not sampled were pruned. Some of the studied museum specimens were only determined up to the genus level. In that case, if it was the only sampled species of the genus, simply one of the species included in the TOL was chosen. If more species of the genus were sampled, the specimen identified at the genus level was placed at the base of the genus. For the sampled species that were missing from the TOL, and if they were the only included member of the genus, one species of the genus included in the TOL was kept and renamed (all sampled genera were found in the TOL). In the cases of missing species for which co-generic species were sampled as well (six instances), additional sources (see below) to build the corresponding topology and to define the relevant divergence ages were used.

The following species are considered valid (Wilson and Reeder 2005), but are absent from the TOL (Hedges et al. 2015):

Chinchilla chinchilla: as the other species of the genus is included and present in the TOL, and as we were not able to find a divergence time for *Chinchilla*, we placed the latter at an intermediate position.

Lepus whythei: *L. victoria*, including the subspecies *L. v. whythei*, was considered as cospecific with *L. saxatilis* [Robinson and Dippenaar (1987) *in* (Chapman and Flux 1990)]. We hence used the latter species.

Paraechinus micropus: as another species of this genus was included and found in the TOL, we used the divergence time of the genus [ca. 2.5 Ma; (Bannikova et al. 2014)]

Pteropus pselaphon: Due to incompatibility with the *Pteropus* topology of the TOL and that of Almeida et al. (2014), and given that the branch lengths within among the sampled species were null anyways (except for the *P. giganteus*-*P. vampyrus* clade), we placed *P. pselaphon* in a polytomy at the base of the genus.

Tragulus kanchil: as another species of the genus (*T. javanicus*) is included and present in the TOL, and as we were not able to find a phylogeny with divergence time including these two species, we placed *T. kanchil* at an intermediate position on the *Tragulus* branch (which is roughly the divergence time of the *T. javanicus*-*T. napu* of the TOL).

Vulpes pallida: *V. pallida* is regarded as the sister-taxon of *V. chama* (Nyakatura and Bininda-Emonds 2012), which is included in the TOL but not in our sampling. We will hence use the position of the latter.

The resulting timetree is given as a supplementary NEXUS file.

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Table S1 Number of specimens, species, and genera included in the study

Taxon	specimens	species	genera
Afrosoricida	12	6	6
Carnivora	76	56	47
Cetartiodactyla	78	57	45
Chiroptera	21	19	13
Dermoptera	2	2	2
Eulipotyphla	35	21	14
Hyracoidea	8	4	3
Lagomorpha	15	12	4
Macroscelidea	10	7	3
Marsupialia	43	32	25
Monotremata	5	3	3
Perissodactyla	7	6	2
Pholidota	4	4	1
Primates	49	43	33
Proboscidea	2	1	1
Rodentia	75	63	58
Scandentia	6	4	1
Sirenia	3	1	1
Tubulidenta	2	1	1
Xenarthra	14	10	9
Total	**467**	**352**	**272**

Table S2 List of collection specimens included in the study

Institutional Abbreviations:

GMS	Hospital of Small Animal Surgery, University Giessen
NME	Naturkundemuseum Erfurt
PMJ	Phyletisches Museum Jena
SMF	Senckenberg Forschungsinstitut und Naturkundemuseum Frankfurt
SMNS	Staatliches Museum für Naturkunde
ZMB	Museum für Naturkunde – Leibniz-Institut für Evolutions- und Biodiversitätsforschung zu Berlin

collection number	Clade	Species
GießenMS03	Carnivora	*Nasua nasua*
GießenMS02	Carnivora	*Zalophus californianus*
GießenMS01	Marsupialia	*Dasyurus viverrinus*
NME_M2092/12	Carnivora	*Acinonyx jubatus*
NME_M480/95	Carnivora	*Leptailurus serval*
NME_M891/01	Carnivora	*Lynx lynx*
NME_M2110/13	Carnivora	*Martes foina*
NME_M2111/13	Carnivora	*Martes foina*
NME_M2107/13	Carnivora	*Martes martes*
NME_M2784	Carnivora	*Martes martes*
NME_1995/10	Carnivora	*Panthera tigris*
NME_M1832/08	Carnivora	*Prionailurus bengalensis*
NME_M2115/13	Carnivora	*Prionailurus bengalensis*
NME_M2112/13	Carnivora	*Puma concolor*
NME_M2068/12	Carnivora	*Vulpes vulpes*
NME_M2113/13	Carnivora	*Vulpes vulpes*
NME_M985/04	Cetartiodactyla	*Tragulus javanicus*
NME_MX1	Chiroptera	*Rousettus aegyptiacus*
NME_M989/04	Marsupialia	*Bettongia penicillata*
NME_MX2	Marsupialia	*Macropus rufogriseus*
NME_M148/92	Primates	*Macaca mulatta*
NME_M994/05	Primates	*Saguinus oedipus*
NME_M721/96	Rodentia	*Cricetus cricetus*
PMJ_Mam6274	Afrosoricida	*Echinops telfairi*
PMJ_Mam6285	Afrosoricida	*Echinops telfairi*
PMJ_Mam5892	Afrosoricida	*Hemicentetes semispinosus*
PMJ_Mam5893	Afrosoricida	*Hemicentetes semispinosus*
PMJ_Mam5897	Afrosoricida	*Microgale talazaci*
PMJ_Mam6270	Afrosoricida	*Setifer setosus*

collection number	Clade	Species
PMJ_Mam6281	Afrosoricida	*Setifer setosus*
PMJ_Mam4205	Afrosoricida	*Tenrec ecaudatus*
PMJ_Mam5904	Afrosoricida	*Tenrec ecaudatus*
PMJ_Mam6299	Afrosoricida	*Tenrec ecaudatus*
PMJ_Mam6639	Carnivora	*Ailurus fulgens*
PMJ_Mam6856	Carnivora	*Ailurus fulgens*
PMJ_Mam2939	Carnivora	*Aonyx cinerea*
PMJ_Mam2874	Carnivora	*Arctictis binturong*
PMJ_Mam2876	Carnivora	*Atilax paludinosus*
PMJ_Mam2997	Carnivora	*Canis lupus*
PMJ_Mam2991	Carnivora	*Canis mesomelas*
PMJ_Mam2952	Carnivora	*Chrysocyon brachyurus*
PMJ_Mam2953	Carnivora	*Chrysocyon brachyurus*
PMJ_Mam2954	Carnivora	*Chrysocyon brachyurus*
PMJ_Mam6743	Carnivora	*Crossarchus obscurus*
PMJ_Mam2965	Carnivora	*Cuon alpinus*
PMJ_Mam2870	Carnivora	*Cynictis penicillata*
PMJ_Mam2877	Carnivora	*Cynogale bennettii*
PMJ_Mam6896	Carnivora	*Felis nigripes*
PMJ_Mam8161	Carnivora	*Felis silvestris*
PMJ_Mam2866	Carnivora	*Galerella pulverulenta*
PMJ_Mam6617	Carnivora	*Galictis vittata*
PMJ_Mam6734	Carnivora	*Galidia elegans*
PMJ_Mam2851	Carnivora	*Genetta genetta*
PMJ_Mam2853	Carnivora	*Genetta genetta*
PMJ_Mam2856	Carnivora	*Genetta genetta*
PMJ_Mam2858	Carnivora	*Genetta tigrina*
PMJ_Mam2875	Carnivora	*Helogale parvula*
PMJ_Mam6679	Carnivora	*Hemigalus derbyanus*
PMJ_Mam6681	Carnivora	*Hemigalus derbyanus*
PMJ_Mam2859	Carnivora	*Herpestes ichneumon*
PMJ_Mam2957	Carnivora	*Hyaena hyaena*
PMJ_Mam2868	Carnivora	*Ichneumia albicauda*
PMJ_Mam6863	Carnivora	*Ictonyx libyca*
PMJ_Mam6864	Carnivora	*Ictonyx libyca*
PMJ_Mam2942	Carnivora	*Lutra lutra*
PMJ_Mam8030	Carnivora	*Lutra lutra*
PMJ_Mam2943	Carnivora	*Lutrogale perspicillata*
PMJ_Mam2425	Carnivora	*Meles meles*
PMJ_Mam7929	Carnivora	*Meles meles*
PMJ_Mam22	Carnivora	*Mustela erminea*
PMJ_Mam363	Carnivora	*Mustela erminea*
PMJ_Mam2382	Carnivora	*Mustela nivalis*
PMJ_Mam2948	Carnivora	*Mustela nudipes*
PMJ_Mam2949	Carnivora	*Mustela nudipes*
PMJ_Mam563	Carnivora	*Mustela putorius*
PMJ_Mam2958	Carnivora	*Nasua nasua*

collection number	Clade	Species
PMJ_Mam2959	Carnivora	*Nasua nasua*
PMJ_Mam2109	Carnivora	*Nyctereutes procyonoides*
PMJ_Mam935	Carnivora	*Otaria byronia*
PMJ_Mam2848	Carnivora	*Otocolobus manul*
PMJ_Mam6618	Carnivora	*Otocyon megalotis*
PMJ_Mam6274	Carnivora	*Phoca groenlandica*
PMJ_Mam4872	Carnivora	*Phoca vitulina*
PMJ_Mam628	Carnivora	*Phoca vitulina*
PMJ_Mam2961	Carnivora	*Potos flavus*
PMJ_Mam7413	Carnivora	*Potos flavus*
PMJ_Mam6673	Carnivora	*Prionodon linsang*
PMJ_Mam8037	Carnivora	*Procyon lotor*
PMJ_Mam6651	Carnivora	*Pusa sibirica*
PMJ_Mam5129	Carnivora	*Ursus arctos*
PMJ_Mam1714	Carnivora	*Viverra tangalunga*
PMJ_Mam2945	Carnivora	*Vormela peregusna*
PMJ_Mam6873	Carnivora	*Vormela peregusna*
PMJ_Mam6629	Carnivora	*Vulpes pallida*
PMJ_Mam597	Cetartiodactyla	*Capra aegagrus*
PMJ_Mam7931	Cetartiodactyla	*Capra aegagrus*
PMJ_Mam3326	Cetartiodactyla	*Litocranius walleri*
PMJ_Mam3327	Cetartiodactyla	*Litocranius walleri*
PMJ_Mam3366	Cetartiodactyla	*Madoqua guentheri*
PMJ_Mam3332	Cetartiodactyla	*Madoqua saltiana*
PMJ_Mam7132	Cetartiodactyla	*Muntiacus reevesi*
PMJ_Mam2297	Cetartiodactyla	*Oreamnos americanus*
PMJ_Mam3322	Cetartiodactyla	*Oreotragus oreotragus*
PMJ_Mam3323	Cetartiodactyla	*Oreotragus oreotragus*
PMJ_Mam3328	Cetartiodactyla	*Pelea capreolus*
PMJ_Mam3325	Cetartiodactyla	*Raphicerus campestris*
PMJ_Mam596	Cetartiodactyla	*Rupicapra rupicapra*
PMJ_Mam7257	Cetartiodactyla	*Tragulus javanicus*
PMJ_Mam7237	Cetartiodactyla	*Tragulus kanchil*
PMJ_Mam7238	Cetartiodactyla	*Tragulus kanchil*
PMJ_Mam98	Chiroptera	*Barbastella barbastellus*
PMJ_Mam2145	Chiroptera	*Eptesicus serotinus*
PMJ_Mam414	Chiroptera	*Eptesicus serotinus*
PMJ_Mam104	Chiroptera	*Miniopterus schreibersii*
PMJ_Mam8003	Chiroptera	*Myotis daubentonii*
PMJ_Mam5058	Chiroptera	*Myotis nattereri*
PMJ_Mam6505	Chiroptera	*Nyctalus noctula*
PMJ_Mam109	Chiroptera	*Plecotus auritus*
PMJ_Mam7977	Chiroptera	*Plecotus austriacus*
PMJ_Mam8114	Chiroptera	*Pteropus alecto*
PMJ_Mam2152	Chiroptera	*Pteropus giganteus*
PMJ_Mam3530	Chiroptera	*Pteropus vampyrus*
PMJ_Mam7980	Chiroptera	*Rhinolophus hipposideros*

collection number	Clade	Species
PMJ_Mam6502	Chiroptera	*Saccolaimus saccolaimus*
PMJ_Mam665	Dermoptera	*Cynocephalus volans*
PMJ_Mam6412	Dermoptera	*Galeopterus variegatus*
PMJ_Mam6258	Eulipotyphla	*Echinosorex gymnura*
PMJ_Mam6293	Eulipotyphla	*Echinosorex gymnura*
PMJ_Mam6296	Eulipotyphla	*Echinosorex gymnura*
PMJ_Mam74	Eulipotyphla	*Erinaceus europaeus*
PMJ_Mam6308	Eulipotyphla	*Hemiechinus auritus*
PMJ_Mam4348	Eulipotyphla	*Hylomys suillus*
PMJ_Mam5911	Eulipotyphla	*Hylomys suillus*
PMJ_Mam7342	Eulipotyphla	*Paraechinus aethiopicus*
PMJ_Mam6259	Eulipotyphla	*Paraechinus micropus*
PMJ_Mam4769	Eulipotyphla	*Solenodon paradoxus*
PMJ_Mam7414	Eulipotyphla	*Solenodon paradoxus*
PMJ_Mam5914	Eulipotyphla	*Suncus etruscus*
PMJ_Mam103	Eulipotyphla	*Talpa europaea*
PMJ_Mam6418	Hyracoidea	*Procavia capensis*
PMJ_Mam1157	Lagomorpha	*Lepus europaeus*
PMJ_Mam618	Lagomorpha	*Lepus europaeus*
PMJ_Mam2131	Lagomorpha	*Lepus timidus*
PMJ_Mam35	Lagomorpha	*Lepus timidus*
PMJ_Mam44	Lagomorpha	*Oryctolagus cuniculus*
PMJ_Mam619	Lagomorpha	*Oryctolagus cuniculus*
PMJ_Mam6321	Macroscelidea	*Elephantulus intufi*
PMJ_Mam921	Marsupialia	*Aepyprymnus rufescens*
PMJ_Mam6552	Marsupialia	*Chironectes minimus*
PMJ_Mam262	Marsupialia	*Dasyurus spec.*
PMJ_Mam6603	Marsupialia	*Dendrolagus matschiei*
PMJ_Mam1715	Marsupialia	*Didelphis virginiana*
PMJ_Mam8160	Marsupialia	*Macropus eugenii*
PMJ_Mam634	Marsupialia	*Macropus giganteus*
PMJ_Mam6600	Marsupialia	*Macropus rufogriseus*
PMJ_Mam637	Marsupialia	*Macropus spec.*
PMJ_Mam6584	Marsupialia	*Marmosa spec.*
PMJ_Mam6588	Marsupialia	*Marmosa spec.*
PMJ_Mam6548	Marsupialia	*Petrogale penicillata*
PMJ_Mam1718	Marsupialia	*Phascolarctos cinereus*
PMJ_Mam6598	Marsupialia	*Philander opossum*
PMJ_Mam6553	Marsupialia	*Setonix brachyurus*
PMJ_Mam6602	Marsupialia	*Spilocuscus maculatus*
PMJ_Mam6549	Marsupialia	*Strigocuscus celebensis*
PMJ_Mam6543	Marsupialia	*Thylogale brunii*
PMJ_Mam6560	Marsupialia	*Trichosurus vulpecula*
PMJ_Mam6561	Marsupialia	*Trichosurus vulpecula*
PMJ_Mam6604	Marsupialia	*Wallabia bicolor*
PMJ_Mam4803	Monotremata	*Tachyglossus aculeatus*
PMJ_Mam949	Monotremata	*Tachyglossus aculeatus*

collection number	Clade	Species
PMJ_Mam1412	Perissodactyla	*Equus caballus*
PMJ_Mam7604	Primates	*Aotus trivirgatus*
PMJ_Mam7828	Primates	*Arctocebus calabarensis*
PMJ_Mam3307	Primates	*Cacajao calvus*
PMJ_Mam7562	Primates	*Callicebus moloch*
PMJ_Mam4317	Primates	*Callimico goeldii*
PMJ_Mam7505	Primates	*Callithrix argentata*
PMJ_Mam7499	Primates	*Callithrix geoffroyi*
PMJ_Mam5093	Primates	*Callithrix jacchus*
PMJ_Mam7496	Primates	*Callithrix pygmaea*
PMJ_Mam8025	Primates	*Cebus apella*
PMJ_Mam4043	Primates	*Cercopithecus cephus*
PMJ_Mam7481	Primates	*Cercopithecus diana*
PMJ_Mam7525	Primates	*Chiropotes satanas*
PMJ_Mam3096	Primates	*Chlorocebus aethiops*
PMJ_Mam7808	Primates	*Daubentonia madagascariensis*
PMJ_Mam7388	Primates	*Galago alleni*
PMJ_Mam7837	Primates	*Galago senegalensis*
PMJ_Mam7839	Primates	*Galagoides demidoff*
PMJ_Mam1442	Primates	*Gorilla gorilla*
PMJ_Mam477	Primates	*Gorilla gorilla*
PMJ_Mam516	Primates	*Gorilla gorilla*
PMJ_Mam1380	Primates	*Homo sapiens*
PMJ_Mam1378	Primates	*Hylobates spec.*
PMJ_Mam7531	Primates	*Lagothrix lagotricha*
PMJ_Mam5208	Primates	*Leontopithecus rosalia*
PMJ_Mam376	Primates	*Macaca nigra*
PMJ_Mam541	Primates	*Macaca radiata*
PMJ_Mam563	Primates	*Macaca spec.*
PMJ_Mam1472	Primates	*Mandrillus sphinx*
PMJ_Mam7821	Primates	*Microcebus murinus*
PMJ_Mam3262	Primates	*Nycticebus coucang*
PMJ_Mam7841	Primates	*Otolemur crassicaudatus*
PMJ_Mam7802	Primates	*Perodicticus potto*
PMJ_Mam3259	Primates	*Pithecia monachus*
PMJ_Mam4014	Primates	*Pithecia pithecia*
PMJ_Mam1404	Primates	*Pongo abelii*
PMJ_Mam1440	Primates	*Pongo abelii*
PMJ_Mam1450	Primates	*Pongo abelii*
PMJ_Mam3220	Primates	*Pongo abelii*
PMJ_Mam7514	Primates	*Saguinus fuscicollis*
PMJ_Mam5142	Primates	*Saimiri sciureus*
PMJ_Mam1432	Primates	*Semnopithecus entellus*
PMJ_Mam7809	Primates	*Tarsius syrichta*
PMJ_Mam2469	Primates	*Varecia variegata*
PMJ_Mam1629	Proboscidea	*Elephas maximus*
PMJ_Mam105	Rodentia	*Apodemus sylvaticus*

collection number	Clade	Species
PMJ_Mam6021	Rodentia	*Atlantoxerus getulus*
PMJ_Mam3469	Rodentia	*Bandicota bengalensis*
PMJ_Mam6376	Rodentia	*Bathyergus suillus*
PMJ_Mam6377	Rodentia	*Bathyergus suillus*
PMJ_Mam6379	Rodentia	*Bathyergus suillus*
PMJ_Mam3959	Rodentia	*Callosciurus prevostii*
PMJ_Mam6350	Rodentia	*Callospermophilus lateralis*
PMJ_Mam5885	Rodentia	*Capromys pilorides*
PMJ_Mam2045	Rodentia	*Castor fiber*
PMJ_Mam8164	Rodentia	*Castor fiber*
PMJ_Mam5873	Rodentia	*Chinchilla chinchilla*
PMJ_Mam6049	Rodentia	*Chinchilla lanigera*
PMJ_Mam409	Rodentia	*Chionomys nivalis*
PMJ_Mam2399	Rodentia	*Cricetus cricetus*
PMJ_Mam4054	Rodentia	*Cuniculus paca*
PMJ_Mam6234	Rodentia	*Cynomys ludovicianus*
PMJ_Mam3359	Rodentia	*Dasyprocta leporina*
PMJ_Mam667	Rodentia	*Dasyprocta leporina*
PMJ_Mam2508	Rodentia	*Dicrostonyx torquatus*
PMJ_Mam5886	Rodentia	*Dinomys branickii*
PMJ_Mam3342	Rodentia	*Dolichotis patagonum*
PMJ_Mam3343	Rodentia	*Dolichotis patagonum*
PMJ_Mam2335	Rodentia	*Eliomys quercinus*
PMJ_Mam4752	Rodentia	*Erethizon dorsatum*
PMJ_Mam4724	Rodentia	*Galea musteloides*
PMJ_Mam2476	Rodentia	*Glis glis*
PMJ_Mam6344	Rodentia	*Hydromys chrysogaster*
PMJ_Mam3990	Rodentia	*Hystrix brachyurus*
PMJ_Mam38	Rodentia	*Hystrix cristata*
PMJ_Mam3358	Rodentia	*Hystrix indica*
PMJ_Mam3357	Rodentia	*Lagidium peruanum*
PMJ_Mam6381	Rodentia	*Lagidium peruanum*
PMJ_Mam3356	Rodentia	*Lagostomus maximus*
PMJ_Mam2487	Rodentia	*Lemmus lemmus*
PMJ_Mam620	Rodentia	*Marmota marmota*
PMJ_Mam396	Rodentia	*Microtus arvalis*
PMJ_Mam86	Rodentia	*Muscardinus avellanarius*
PMJ_Mam3355	Rodentia	*Myocastor coypus*
PMJ_Mam621	Rodentia	*Myocastor coypus*
PMJ_Mam102	Rodentia	*Myodes glareolus*
PMJ_Mam4882	Rodentia	*Octodon degus*
PMJ_Mam3349	Rodentia	*Pedetes capensis*
PMJ_Mam6367	Rodentia	*Pedetes capensis*
PMJ_Mam3363	Rodentia	*Petaurista petaurista*
PMJ_Mam5773	Rodentia	*Petinomys setosus*
PMJ_Mam2475	Rodentia	*Rattus norvegicus*
PMJ_Mam3361	Rodentia	*Ratufa affinis*

collection number	**Clade**	**Species**
PMJ_Mam3364	Rodentia	*Rhizomys pruinosus*
PMJ_Mam5754	Rodentia	*Rhizomys pruinosus*
PMJ_Mam87	Rodentia	*Sciurus vulgaris*
PMJ_Mam106	Rodentia	*Spermophilus citellus*
PMJ_Mam94	Rodentia	*Spermophilus citellus*
PMJ_Mam6022	Rodentia	*Tamias sibiricus*
PMJ_Mam3714	Rodentia	*Tatera indica*
PMJ_Mam3365	Rodentia	*Xerus inauris*
PMJ_Mam4270	Scandentia	*Tupaia belangeri*
PMJ_Mam1351	Scandentia	*Tupaia javanica*
PMJ_Mam7779	Scandentia	*Tupaia minor*
PMJ_Mam7792	Scandentia	*Tupaia tana*
PMJ_Mam4122	Tubulidenta	*Orycteropus afer*
PMJ_Mam3522	Xenarthra	*Cabassous unicinctus*
PMJ_Mam3523	Xenarthra	*Dasypus novemcinctus*
PMJ_Mam6454	Xenarthra	*Dasypus novemcinctus*
PMJ_Mam6441	Xenarthra	*Tamandua tetradactyla*
PMJ_Mam6444	Xenarthra	*Tamandua tetradactyla*
SMF_1834	Cetartiodactyla	*Alces alces*
SMF_63162	Chiroptera	*Eonycteris spec.*
SMF_51666	Chiroptera	*Epomophorus gambianus*
SMF_19963	Eulipotyphla	*Crocidura russula*
SMF_49183	Eulipotyphla	*Sorex cinereus*
SMF_77918	Eulipotyphla	*Sorex trowbridgii*
SMF_1477	Hyracoidea	*Procavia capensis*
SMF_21330	Hyracoidea	*Procavia capensis*
SMF_86264	Lagomorpha	*Lepus habessinicus*
SMF_13381	Lagomorpha	*Sylvilagus floridanus*
SMF_47782	Macroscelidea	*Elephantulus rozeti*
SMF_51645	Macroscelidea	*Elephantulus rozeti*
SMF_37573	Macroscelidea	*Petrodromus tetradactylus*
SMF_88586	Macroscelidea	*Petrodromus tetradactylus*
SMF_4661	Macroscelidea	*Rhynchocyon cirnei*
SMF_87191	Macroscelidea	*Rhynchocyon cirnei*
SMF_90470	Marsupialia	*Dactylopsila trivirgata*
SMF_41105	Marsupialia	*Didelphis aurita*
SMF_92337	Pholidota	*Manis tricuspis*
SMF_59359	Primates	*Callithrix pygmaea*
SMF_59233	Primates	*Miopithecus talapoin*
SMF_87415	Rodentia	*Gerbillus latastei*
SMF_92625	Rodentia	*Kerodon rupestris*
SMF_92328	Rodentia	*Thryonomys swinderianus*
SMF_95433	Xenarthra	*Chaetophractus vellerosus*
SMF_94961	Xenarthra	*Chlamyphorus truncatus*
SMF_21091	Xenarthra	*Cyclopes didactylus*
SMF_93390	Xenarthra	*Cyclopes didactylus*
SMF_42286	Xenarthra	*Priodontes maximus*

collection number	**Clade**	**Species**
SMF_41103	Xenarthra	*Tolypeutes matacus*
SMF_44390	Xenarthra	*Tolypeutes tricinctus*
SMNS_32586	Afrosoricida	*Chrysochloris asiatica*
SMNS_43605	Eulipotyphla	*Crocidura leucodon*
SMNS_46074	Eulipotyphla	*Crocidura russula*
SMNS_46095	Eulipotyphla	*Crocidura russula*
SMNS_43670	Eulipotyphla	*Neomys fodiens*
SMNS_46171	Eulipotyphla	*Neomys fodiens*
SMNS_46072	Eulipotyphla	*Sorex araneus*
SMNS_46427	Eulipotyphla	*Sorex araneus*
SMNS_46389	Eulipotyphla	*Sorex coronatus*
SMNS_46864	Eulipotyphla	*Sorex coronatus*
SMNS_40985	Eulipotyphla	*Sorex minutus*
SMNS_43579	Eulipotyphla	*Sorex minutus*
SMNS_18010	Hyracoidea	*Heterohyrax brucei*
SMNS_7408	Primates	*Avahi laniger*
SMNS_39749	Rodentia	*Arvicola amphibius*
SMNS_33773	Rodentia	*Echimys chrysurus*
SMNS_34439	Rodentia	*Ellobius talpinus*
SMNS_2143	Rodentia	*Lophiomys imhausi*
SMNS_33772	Rodentia	*Makalata didelphoides*
SMNS_33932	Rodentia	*Neotoma cinerea*
SMNS_33775	Rodentia	*Proechimys guyannensis*
SMNS_42023	Scandentia	*Tupaia belangeri*
SMNS_46975	Scandentia	*Tupaia belangeri*
SMNS_35291	Xenarthra	*Cyclopes didactylus*
ZMB_MAM_36074	Afrosoricida	*Tenrec ecaudatus*
ZMB_MAM_77216	Cetartiodactyla	*Antilocapra americana*
ZMB_MAM_14817	Cetartiodactyla	*Axis porcinus*
ZMB_MAM_7233	Cetartiodactyla	*Babyrousa babyrussa*
ZMB_MAM_X08	Cetartiodactyla	*Balaenoptera acutorostrata*
ZMB_MAM_X11	Cetartiodactyla	*Bison spec.*
ZMB_MAM_14758	Cetartiodactyla	*Bubalus depressicornis*
ZMB_MAM_971	Cetartiodactyla	*Camelus dromedarius*
ZMB_MAM_X01	Cetartiodactyla	*Capra sibirica*
ZMB_MAM_47492	Cetartiodactyla	*Capricornis spec.*
ZMB_MAM_7945	Cetartiodactyla	*Cephalophus ogilbyi*
ZMB_MAM_714	Cetartiodactyla	*Cephalophus rufilatus*
ZMB_MAM_14722	Cetartiodactyla	*Cephalophus spec.*
ZMB_MAM_14745	Cetartiodactyla	*Cephalophus spec.*
ZMB_MAM_X02	Cetartiodactyla	*Cephalophus spec.*
ZMB_MAM_77254	Cetartiodactyla	*Giraffa camelopardalis*
ZMB_MAM_84969	Cetartiodactyla	*Giraffa camelopardalis*
ZMB_MAM_3391	Cetartiodactyla	*Hemitragus jemlahicus*
ZMB_MAM_68731	Cetartiodactyla	*Hemitragus jemlahicus*
ZMB_MAM_77242	Cetartiodactyla	*Hexaprotodon liberiensis*
ZMB_MAM_44221	Cetartiodactyla	*Hippopotamus amphibius*

collection number	Clade	Species
ZMB_MAM_X03	Cetartiodactyla	*Hippopotamus amphibius*
ZMB_MAM_77265	Cetartiodactyla	*Hippotragus equinus*
ZMB_MAM_41500	Cetartiodactyla	*Inia geoffrensis*
ZMB_MAM_51863	Cetartiodactyla	*Kobus ellipsiprymnus*
ZMB_MAM_83385	Cetartiodactyla	*Kobus ellipsiprymnus*
ZMB_MAM_16577	Cetartiodactyla	*Kobus kob*
ZMB_MAM_77356	Cetartiodactyla	*Lagenorhynchus acutus*
ZMB_MAM_6257	Cetartiodactyla	*Lama guanicoe*
ZMB_MAM_77303	Cetartiodactyla	*Monodon monoceros*
ZMB_MAM_77304	Cetartiodactyla	*Monodon monoceros*
ZMB_MAM_14451	Cetartiodactyla	*Naemorhedus goral*
ZMB_MAM_62086	Cetartiodactyla	*Okapia johnstoni*
ZMB_MAM_70325	Cetartiodactyla	*Okapia johnstoni*
ZMB_MAM_77372	Cetartiodactyla	*Orcinus orca*
ZMB_MAM_67804	Cetartiodactyla	*Ovibos moschatus*
ZMB_MAM_5675	Cetartiodactyla	*Phacochoerus aethiopicus*
ZMB_MAM_A3353	Cetartiodactyla	*Pontoporia blainvillei*
ZMB_MAM_70068	Cetartiodactyla	*Przewalskium albirostris*
ZMB_MAM_14783	Cetartiodactyla	*Pseudois nayaur*
ZMB_MAM_70097	Cetartiodactyla	*Redunca fulvorufula*
ZMB_MAM_70511	Cetartiodactyla	*Redunca fulvorufula*
ZMB_MAM_52975	Cetartiodactyla	*Saiga tatarica*
ZMB_MAM_52977	Cetartiodactyla	*Saiga tatarica*
ZMB_MAM_83383	Cetartiodactyla	*Saiga tatarica*
ZMB_MAM_5097	Cetartiodactyla	*Steno bredanensis*
ZMB_MAM_25745	Cetartiodactyla	*Sus scrofa*
ZMB_MAM_4423	Cetartiodactyla	*Sus scrofa*
ZMB_MAM_X04	Cetartiodactyla	*Sus verrucosus*
ZMB_MAM_1196	Cetartiodactyla	*Tayassu pecari*
ZMB_MAM_7979	Cetartiodactyla	*Tayassu pecari*
ZMB_MAM_77171	Cetartiodactyla	*Tragelaphus angasii*
ZMB_MAM_X05	Cetartiodactyla	*Tragelaphus scriptus*
ZMB_MAM_105251	Cetartiodactyla	*Tragelaphus spec.*
ZMB_MAM_69007	Cetartiodactyla	*Tragelaphus spec.*
ZMB_MAM_X06	Cetartiodactyla	*Tragelaphus spec.*
ZMB_MAM_X07	Cetartiodactyla	*Tragelaphus spec.*
ZMB_MAM_13243	Cetartiodactyla	*Tragelaphus strepsiceros*
ZMB_MAM_66434	Cetartiodactyla	*Tursiops truncatus*
ZMB_MAM_56207	Cetartiodactyla	*Vicugna pacos*
ZMB_MAM_65361	Cetartiodactyla	*Vicugna vicugna*
ZMB_MAM_66825	Chiroptera	*Dobsonia inermis*
ZMB_MAM_89344	Chiroptera	*Pteropus poliocephalus*
ZMB_MAM_88614	Chiroptera	*Pteropus pselaphon*
ZMB_MAM_88424	Chiroptera	*Pteropus vampyrus*
ZMB_MAM_95210	Eulipotyphla	*Blarina brevicauda*
ZMB_MAM_33829	Eulipotyphla	*Desmana moschata*
ZMB_MAM_72232	Eulipotyphla	*Echinosorex gymnura*

collection number	Clade	Species
ZMB_MAM_101380	Eulipotyphla	*Erinaceus europaeus*
ZMB_MAM_94010	Eulipotyphla	*Erinaceus europaeus*
ZMB_MAM_27427	Eulipotyphla	*Erinaceus roumanicus*
ZMB_MAM_37179	Eulipotyphla	*Erinaceus roumanicus*
ZMB_MAM_62455	Eulipotyphla	*Mogera wogura*
ZMB_MAM_21177	Hyracoidea	*Dendrohyrax arboreus*
ZMB_MAM_7579	Hyracoidea	*Dendrohyrax arboreus*
ZMB_MAM_18255	Hyracoidea	*Dendrohyrax dorsalis*
ZMB_MAM_21201	Hyracoidea	*Heterohyrax brucei*
ZMB_MAM_81937	Lagomorpha	*Lepus americanus*
ZMB_MAM_81500	Lagomorpha	*Lepus brachyurus*
ZMB_MAM_47707	Lagomorpha	*Lepus capensis*
ZMB_MAM_81541	Lagomorpha	*Lepus whytei*
ZMB_MAM_72902	Lagomorpha	*Ochotona curzoniae*
ZMB_MAM_81476	Lagomorpha	*Ochotona roylei*
ZMB_MAM_38115	Lagomorpha	*Ochotona rufescens*
ZMB_MAM_84903	Macroscelidea	*Elephantulus brachyrhynchus*
ZMB_MAM_84901	Macroscelidea	*Rhynchocyon petersi*
ZMB_MAM_37018	Macroscelidea	*Rhynchocyon spec.*
ZMB_MAM_44173	Marsupialia	*Ailurops ursinus*
ZMB_MAM_34344	Marsupialia	*Dactylopsila trivirgata*
ZMB_MAM_39313	Marsupialia	*Didelphis marsupialis*
ZMB_MAM_29493	Marsupialia	*Didelphis virginiana*
ZMB_MAM_8551	Marsupialia	*Echymipera spec.*
ZMB_MAM_7878	Marsupialia	*Lasiorhinus latifrons*
ZMB_MAM_84111	Marsupialia	*Lasiorhinus latifrons*
ZMB_MAM_35451	Marsupialia	*Lutreolina crassicaudata*
ZMB_MAM_12139	Marsupialia	*Perameles nasuta*
ZMB_MAM_16070	Marsupialia	*Perameles nasuta*
ZMB_MAM_2499	Marsupialia	*Petauroides volans*
ZMB_MAM_73246	Marsupialia	*Petrogale spec.*
ZMB_MAM_36037	Marsupialia	*Phascolarctos cinereus*
ZMB_MAM_38061	Marsupialia	*Philander opossum*
ZMB_MAM_3610	Marsupialia	*Sarcophilus harrisii*
ZMB_MAM_8946	Marsupialia	*Spilocuscus maculatus*
ZMB_MAM_X09	Marsupialia	*Trichosurus vulpecula*
ZMB_MAM_31041	Monotremata	*Ornithorhynchus anatinus*
ZMB_MAM_36004	Monotremata	*Ornithorhynchus anatinus*
ZMB_MAM_47555	Monotremata	*Zaglossus bruijni*
ZMB_MA'M_69006	Perissodactyla	*Equus asinus*
ZMB_MAM_53127	Perissodactyla	*Equus burchellii*
ZMB_MAM_60363	Perissodactyla	*Equus caballus*
ZMB_MAM_105723	Perissodactyla	*Equus kiang*
ZMB_MAM_4950	Perissodactyla	*Tapirus indicus*
ZMB_MAM_62085	Perissodactyla	*Tapirus pinchaque*
ZMB_MAM_60539	Pholidota	*Manis javanica*
ZMB_MAM_75095	Pholidota	*Manis pentadactyla*

collection number	Clade	Species
ZMB_MAM_73506	Pholidota	*Manis temminckii*
ZMB_MAM_89830	Proboscidea	*Elephas maximus*
ZMB_MAM_8319	Rodentia	*Abrocoma spec.*
ZMB_MAM_5371	Rodentia	*Cricetomys emini*
ZMB_MAM_18180	Rodentia	*Ctenomys tucumanus*
ZMB_MAM_8345	Rodentia	*Echimys spec.*
ZMB_MAM_75654	Rodentia	*Georychus capensis*
ZMB_MAM_X10	Rodentia	*Heliophobius spec.*
ZMB_MAM_85102	Rodentia	*Lophiomys imhausi*
ZMB_MAM_26655	Rodentia	*Nectomys squamipes*
ZMB_MAM_38308	Sirenia	*Dugong dugon*
ZMB_MAM_38316	Sirenia	*Dugong dugon*
ZMB_MAM_38340	Sirenia	*Dugong dugon*
ZMB_MAM_84695	Tubulidenta	*Orycteropus afer*
ZMB_MAM_77025	Xenarthra	*Myrmecophaga tridactyla*

Table S3 Data on individual vertebral lengths [mm], overall cervical spine length [mm], tibial length [mm], and body weight [kg]

Clade	Family	Species	C1	C2	C3	C4	C5	C6	C7	Cervical spine	Tibia	Body weight
Afrosoricida	Chrysochloridae	*Chrysochloris asiatica*	1.38	3.11	1.41	1.07	1.02	1.03	1.49	10.51	13.01	0.470
Afrosoricida	Tenrecidae	*Echinops telfairi*	1.41	2.82	1.91	1.79	1.72	1.74	1.65	13.02	24.57	0.180
Afrosoricida	Tenrecidae	*Hemicentetes semispinosus*	1.22	3.77	2.37	2.13	1.80	1.74	1.54	14.57	26.67	0.180
Afrosoricida	Tenrecidae	*Microgale talazaci*	0.80	3.02	2.08	1.89	1.65	1.57	1.36	12.37		0.050
Afrosoricida	Tenrecidae	*Setifer setosus*	1.27	3.13	2.05	1.99	1.78	1.71	1.73	13.64	24.42	0.225
Afrosoricida	Tenrecidae	*Tenrec ecaudatus*	2.87	7.61	4.53	4.22	3.82	3.61	3.15	29.81	56.65	0.900
Carnivora	Ailuridae	*Ailurus fulgens*	5.67	16.21	8.35	8.34	8.29	7.86	7.71	62.42	118.71	4.325
Carnivora	Canidae	*Canis lupus*	12.25	36.26	30.84	27.11	25.45	23.05	21.97	176.93	219.49	26.625
Carnivora	Canidae	*Canis mesomelas*	6.04	35.82	23.75	23.50	19.51	16.00	13.08	137.70	95.50	10.250
Carnivora	Canidae	*Chrysocyon brachyurus*	10.90	50.23	34.04	32.59	28.88	24.53	20.08	201.25	259.91	21.500
Carnivora	Canidae	*Cuon alpinus*	7.22	36.70	23.88	23.12	20.40	19.41	16.22	146.95	113.53	15.750
Carnivora	Canidae	*Nyctereutes procyonoides*	6.30	25.64	17.47	17.10	15.02	13.46	10.98	105.97	93.66	6.500
Carnivora	Canidae	*Otocyon megalotis*	4.92	19.26	11.56	12.12	11.04	10.14	8.07	77.11	106.81	4.150
Carnivora	Canidae	*Vulpes pallida*	2.92	17.38	11.73	11.23	10.30	10.05	8.11	71.72	149.97	2.800
Carnivora	Canidae	*Vulpes vulpes*	5.68	24.21	17.15	16.71	15.65	14.67	11.98	106.03	84.54	4.123
Carnivora	Eupleridae	*Galidia elegans*	2.69	11.36	6.99	6.72	6.69	6.21	5.70	46.36	78.60	0.800
Carnivora	Felidae	*Acinonyx jubatus*	12.00	38.36	25.63	24.35	22.78	22.26	17.89	163.27	85.95	53.500
Carnivora	Felidae	*Felis nigripes*	3.38	14.28	8.63	8.63	8.11	7.79	7.04	57.86	105.55	2.125
Carnivora	Felidae	*Felis silvestris*	3.77	17.64	11.99	11.08	10.71	8.82	8.30	72.31		5.500
Carnivora	Felidae	*Leptailurus serval*	6.47	18.13	7.67	6.99	4.90	5.65	7.00	56.81	229.57	13.350
Carnivora	Felidae	*Lynx lynx*	9.43	30.12	19.46	17.30	16.95	17.00	15.20	125.46	39.95	23.000
Carnivora	Felidae	*Otocolobus manul*	3.25	15.60	8.50	7.13	7.58	7.39	7.05	56.50	73.10	3.500
Carnivora	Felidae	*Panthera tigris*	21.41	62.30	36.47	30.37	28.33	29.22	28.05	236.15		119.700
Carnivora	Felidae	*Prionailurus bengalensis*	3.98	16.60	10.21	9.85	9.22	9.14	8.01	66.99	203.03	5.000
Carnivora	Felidae	*Puma concolor*	7.06	21.86	13.95	13.55	13.45	11.57	11.80	93.24	138.98	7.000

Clade	Family	Species	C1	C2	C3	C4	C5	C6	C7	Cervical spine	Tibia	Body weight
Carnivora	Herpestidae	*Atilax paludinosus*	3.44	17.36	10.08	9.92	10.00	9.50	8.70	69.00	40.70	3.300
Carnivora	Herpestidae	*Crossarchus obscurus*	2.93	11.63	6.20	5.98	6.10	6.05	5.74	44.63	87.18	0.790
Carnivora	Herpestidae	*Cynictis penicillata*	2.44	10.87	7.50	7.50	7.48	6.35	5.21	47.35	64.12	0.599
Carnivora	Herpestidae	*Galerella pulverulenta*	1.79	12.33	7.42	7.50	8.20	7.11	6.40	50.75	107.06	0.650
Carnivora	Herpestidae	*Helogale parvula*	1.81	7.98	5.22	4.95	4.94	4.60	3.89	33.39	66.50	0.275
Carnivora	Herpestidae	*Herpestes ichneumon*	4.60	20.88	11.74	11.65	11.37	10.86	9.29	80.39	53.78	2.200
Carnivora	Herpestidae	*Ichneumia albicauda*	3.55	20.83	13.41	13.26	12.88	12.13	10.26	86.32	99.26	3.500
Carnivora	Hyaenidae	*Hyaena hyaena*	15.99	47.57	26.84	26.80	26.76	27.45	21.68	193.09	60.42	40.000
Carnivora	Mustelidae	*Aonyx cinerea*	3.38	9.68	7.87	7.37	6.87	6.86	7.74	49.77	218.75	3.000
Carnivora	Mustelidae	*Galictis vittata*	4.12	15.33	11.73	11.72	11.15	10.81	10.22	75.08	72.47	2.300
Carnivora	Mustelidae	*Ictonyx libyca*	2.44	7.16	5.14	4.84	4.64	4.81	4.49	33.50	36.45	0.425
Carnivora	Mustelidae	*Lutra lutra*	4.39	15.86	11.31	11.40	11.30	11.94	11.42	77.60	62.16	6.750
Carnivora	Mustelidae	*Lutrogale perspicillata*	5.39	18.73	12.89	13.22	14.20	13.52	13.50	91.45	63.90	9.000
Carnivora	Mustelidae	*Martes foina*	3.50	13.30	8.60	8.72	8.59	7.82	7.70	58.22	34.68	1.700
Carnivora	Mustelidae	*Martes martes*	2.89	14.40	9.35	8.97	8.84	8.19	8.15	60.77	109.20	1.300
Carnivora	Mustelidae	*Meles meles*	7.99	22.44	14.46	13.62	13.41	13.20	12.76	97.86	101.41	13.000
Carnivora	Mustelidae	*Mustela erminea*	1.37	7.49	5.66	5.77	5.74	5.44	4.74	36.18	41.34	0.110
Carnivora	Mustelidae	*Mustela nivalis*	1.31	5.59	4.20	4.26	4.12	3.88	3.61	26.97	57.92	0.047
Carnivora	Mustelidae	*Mustela nudipes*	2.69	12.14	8.96	8.80	8.65	7.91	7.81	56.94	64.95	1.000
Carnivora	Mustelidae	*Mustela putorius*	3.07	9.62	7.06	6.83	6.68	6.81	6.30	46.37	43.68	0.809
Carnivora	Mustelidae	*Vormela peregusna*	2.42	9.18	7.34	7.24	6.92	6.76	6.55	46.40	33.13	0.543
Carnivora	Otariidae	*Otaria byronia*	16.24	37.42	33.49	36.71	39.43	39.99	38.00	241.28	167.09	207.500
Carnivora	Otariidae	*Zalophus californianus*	9.93	29.47	24.00	24.89	26.00	27.43	26.15	167.87		180.000
Carnivora	Phocidae	*Phoca groenlandica*	9.59	27.87	20.67	20.22	20.07	22.98	21.87	143.27	127.35	180.000
Carnivora	Phocidae	*Phoca vitulina*	10.39	34.84	27.84	28.78	28.78	30.07	25.51	186.21	53.84	115.000
Carnivora	Phocidae	*Pusa sibirica*	4.54	22.02	14.41	14.11	14.21	15.46	12.91	97.66	216.23	90.000
Carnivora	Prionodontidae	*Prionodon linsang*	5.46	17.97	12.53	12.52	12.50	12.17	9.82	82.97	81.50	0.700
Carnivora	Procyonidae	*Nasua nasua*	5.27	13.01	7.67	7.31	7.02	7.93	7.54	55.75	97.27	4.750
Carnivora	Procyonidae	*Potos flavus*	6.04	11.92	6.15	5.73	5.70	5.79	6.08	47.39	104.55	3.000

Clade	Family	Species	C1	C2	C3	C4	C5	C6	C7	Cervical spine	Tibia	Body weight
Carnivora	Procyonidae	*Procyon lotor*	5.58	13.68	6.54	6.53	6.47	6.47	6.30	51.57	91.72	6.000
Carnivora	Ursidae	*Ursus arctos*	22.66	44.86	24.79	22.36	22.03	22.25	17.92	176.87		277.500
Carnivora	Viverridae	*Arctictis binturong*	7.70	17.44	9.31	8.79	8.35	8.60	7.60	67.79	91.36	12.250
Carnivora	Viverridae	*Cynogale bennettii*	8.15	22.52	13.56	13.38	12.88	13.17	11.96	95.62	112.85	4.000
Carnivora	Viverridae	*Genetta genetta*	4.04	18.36	13.16	12.77	13.07	12.19	10.04	83.64	117.73	1.867
Carnivora	Viverridae	*Genetta tigrina*	5.01	19.15	14.11	14.03	13.99	11.71	10.97	88.97	83.83	1.820
Carnivora	Viverridae	*Hemigalus derbyanus*	5.49	20.30	12.42	12.42	11.94	11.07	9.35	82.99	89.26	2.400
Carnivora	Viverridae	*Viverra tangalunga*	6.52	24.06	16.32	16.53	15.50	14.68	11.22	104.83	66.80	7.350
Cetartiodactyla	Antilocapridae	*Antilocapra americana*	22.70	38.00	19.25	16.83	14.20	8.18	6.05	125.21	216.50	46.100
Cetartiodactyla	Balaenopteridae	*Balaenoptera acutorostrata*	47.89	28.92	18.80	24.07	18.28	24.13	27.07	189.16		7500.000
Cetartiodactyla	Bovidae	*Bison spec.*	41.31	82.75	48.83	48.36	50.16	40.43	35.51	347.35	309.50	630.000
Cetartiodactyla	Bovidae	*Bubalus depressicornis*	25.16	62.22	40.21	39.31	38.38	36.58	28.08	269.94	291.00	155.000
Cetartiodactyla	Bovidae	*Capra aegagrus*	27.20	44.14	30.18	28.36	26.31	21.30	12.87	190.34	235.00	61.000
Cetartiodactyla	Bovidae	*Capra sibirica*	44.32	65.04	42.03	40.44	39.18	33.20	21.79	286.00	161.00	130.000
Cetartiodactyla	Bovidae	*Capricornis spec.*	23.16	50.15	35.95	35.10	34.99	30.61	19.77	229.73	159.00	95.000
Cetartiodactyla	Bovidae	*Cephalophus ogilbyi*	16.06	31.61	21.52	20.97	18.43	17.19	12.48	138.26	130.72	19.000
Cetartiodactyla	Bovidae	*Cephalophus rufilatus*	9.08	24.41	19.34	18.09	16.60	14.36	10.25	112.13	113.41	13.000
Cetartiodactyla	Bovidae	*Cephalophus spec.*	9.26	22.38	16.68	15.89	14.81	12.44	8.82	100.30	211.40	13.000
Cetartiodactyla	Bovidae	*Hemitragus jemlahicus*	32.61	49.17	37.97	35.21	29.35	25.34	14.61	224.25	275.75	35.200
Cetartiodactyla	Bovidae	*Hippotragus equinus*	34.47	62.97	36.90	34.93	31.88	22.94	16.43	240.52	233.00	225.000
Cetartiodactyla	Bovidae	*Kobus ellipsiprymnus*	47.33	69.36	45.15	42.30	36.70	29.53	16.67	287.02	215.44	175.333
Cetartiodactyla	Bovidae	*Kobus kob*	42.26	62.27	54.18	41.84	38.06	33.01	21.69	293.31	256.50	105.000
Cetartiodactyla	Bovidae	*Litocranius walleri*	29.92	45.90	39.40	34.41	31.16	27.73	17.09	225.59	182.25	43.500
Cetartiodactyla	Bovidae	*Madoqua guentheri*	9.06	26.18	21.83	20.32	18.18	14.47	9.79	119.83	126.50	4.550
Cetartiodactyla	Bovidae	*Madoqua saltiana*	8.11	22.51	20.33	18.92	16.19	14.70	10.99	111.75	132.00	4.000
Cetartiodactyla	Bovidae	*Naemorhedus goral*	20.81	43.44	34.03	33.05	30.75	25.90	17.46	205.44	250.00	31.750
Cetartiodactyla	Bovidae	*Oreamnos americanus*	22.64	37.27	24.29	23.57	19.00	15.40	10.70	152.87		90.000
Cetartiodactyla	Bovidae	*Oreotragus oreotragus*	14.04	35.52	27.87	26.02	24.34	20.36	14.50	162.62	161.50	12.000
Cetartiodactyla	Bovidae	*Ovibos moschatus*	48.12	59.61	38.65	38.48	36.66	32.54	31.85	285.91	275.00	315.000

Clade	Family	Species	C1	C2	C3	C4	C5	C6	C7	Cervical spine	Tibia	Body weight
Cetartiodactyla	Bovidae	*Pelea capreolus*	28.11	50.80	47.89	44.82	40.12	32.15	21.70	265.59	227.00	25.000
Cetartiodactyla	Bovidae	*Pseudois nayaur*	27.03	42.58	32.92	31.75	28.52	18.12	11.77	192.69	174.00	55.000
Cetartiodactyla	Bovidae	*Raphicerus campestris*	12.67	28.63	26.37	25.85	22.43	17.87	12.41	146.23	156.50	13.000
Cetartiodactyla	Bovidae	*Redunca fulvorufula*	29.32	50.95	44.42	40.73	36.97	29.93	17.24	249.54	251.25	30.000
Cetartiodactyla	Bovidae	*Rupicapra rupicapra*	18.51	31.02	24.14	21.90	18.91	14.46	8.44	137.38	212.50	37.500
Cetartiodactyla	Bovidae	*Saiga tatarica*	19.79	34.62	20.72	19.34	15.36	13.67	10.29	133.79	196.83	37.500
Cetartiodactyla	Bovidae	*Tragelaphus angasii*	23.63	43.19	27.68	25.35	24.38	15.26	9.98	169.47	242.50	120.000
Cetartiodactyla	Bovidae	*Tragelaphus scriptus*	11.69	19.99	13.03	12.65	11.11	6.33	11.58	86.38	168.50	60.000
Cetartiodactyla	Bovidae	*Tragelaphus spec.*	34.52	58.01	42.83	38.27	33.91	26.33	19.13	253.00	212.31	100.000
Cetartiodactyla	Bovidae	*Tragelaphus strepsiceros*	46.70	85.30	51.81	52.97	42.72	25.05	15.55	320.10	249.00	217.500
Cetartiodactyla	Camelidae	*Camelus dromedarius*	61.31	158.20	135.02	132.24	123.61	118.72	66.25	795.35	190.82	434.000
Cetartiodactyla	Camelidae	*Lama guanicoe*	29.55	86.85	91.13	91.17	84.99	66.76	42.60	493.05	242.00	127.500
Cetartiodactyla	Camelidae	*Vicugna pacos*	30.08	87.63	95.66	93.61	84.97	71.78	56.01	519.74	239.50	62.000
Cetartiodactyla	Camelidae	*Vicugna vicugna*	25.10	78.35	90.42	87.73	88.38	72.95	43.70	486.63	339.14	50.000
Cetartiodactyla	Cervidae	*Alces alces*	44.30	80.22	67.00	63.78	62.28	56.35	51.97	425.90	492.54	386.000
Cetartiodactyla	Cervidae	*Axis porcinus*	22.47	51.12	39.40	37.55	32.36	29.18	20.26	232.34	301.33	43.000
Cetartiodactyla	Cervidae	*Muntiacus reevesi*	10.08	20.00	15.43	13.78	13.30	10.00	8.05	90.64	112.50	18.000
Cetartiodactyla	Cervidae	*Przewalskium albirostris*	35.05	63.55	48.05	45.40	43.52	26.82	16.09	278.48	191.10	135.000
Cetartiodactyla	Delphinidae	*Lagenorhynchus acutus*	25.79	6.49	6.25	6.14	6.02	6.05	8.00	64.74		208.000
Cetartiodactyla	Delphinidae	*Orcinus orca*	57.22	8.02	8.11	7.20	6.76	7.81	14.51	109.63		3987.500
Cetartiodactyla	Delphinidae	*Steno bredanensis*	22.57	8.89	4.30	5.76	4.85	6.03	8.49	60.89		114.000
Cetartiodactyla	Delphinidae	*Tursiops truncatus*	30.57	10.35	7.83	7.47	7.10	7.49	7.92	78.73		200.000
Cetartiodactyla	Giraffidae	*Giraffa camelopardalis*	67.25	183.54	158.61	156.89	152.79	124.30	72.86	916.22	390.50	800.000
Cetartiodactyla	Giraffidae	*Okapia johnstoni*	29.76	104.32	70.59	71.01	68.02	63.62	44.18	451.49	316.05	225.000
Cetartiodactyla	Hippopotamidae	*Hexaprotodon liberiensis*	14.61	32.48	16.39	14.72	14.63	14.34	13.64	120.81	277.33	215.000
Cetartiodactyla	Hippopotamidae	*Hippopotamus amphibius*	55.67	78.30	49.57	45.30	46.41	46.52	43.27	365.01	213.00	3750.000
Cetartiodactyla	Iniidae	*Inia geoffrensis*	11.47	9.29	8.25	8.53	8.50	9.10	10.00	65.14		84.000
Cetartiodactyla	Monodontidae	*Monodon monoceros*	39.74	25.49	10.88	10.87	10.94	11.97	12.54	122.42		1250.000
Cetartiodactyla	Pontoporiidae	*Pontoporia blainvillei*	13.01	9.49	6.17	7.19	6.76	7.99	8.93	59.54		40.500

Clade	Family	Species	C1	C2	C3	C4	C5	C6	C7	Cervical spine	Tibia	Body weight
Cetartiodactyla	Suidae	*Babyrousa babyrussa*	14.28	22.70	14.17	13.86	13.63	14.78	16.32	109.74	148.86	71.500
Cetartiodactyla	Suidae	*Phacochoerus aethiopicus*	19.49	30.96	24.86	23.11	22.74	22.79	23.70	167.65	169.03	100.000
Cetartiodactyla	Suidae	*Sus scrofa*	15.59	25.60	18.96	18.09	18.20	19.50	22.28	138.20	198.96	130.000
Cetartiodactyla	Suidae	*Sus verrucosus*	11.91	21.83	14.95	14.61	16.65	17.27	17.70	114.92	148.43	76.000
Cetartiodactyla	Tayassuidae	*Tayassu pecari*	13.05	28.01	15.83	15.92	15.80	15.36	15.06	119.02	208.89	22.000
Cetartiodactyla	Tragulidae	*Tragulus javanicus*	5.33	14.90	9.90	9.69	8.58	7.66	6.30	62.34	104.74	2.850
Cetartiodactyla	Tragulidae	*Tragulus kanchil*	5.75	15.36	11.18	10.57	9.60	8.11	6.78	67.33	93.39	2.000
Chiroptera	Emballonuridae	*Saccolaimus saccolaimus*	0.72	2.23	1.71	1.60	1.56	1.46	1.39	10.67	23.67	0.045
Chiroptera	Pteropodidae	*Dobsonia inermis*	1.33	5.15	3.49	3.43	3.35	3.02	2.58	22.35		0.250
Chiroptera	Pteropodidae	*Eonycteris spec.*	0.65	3.45	2.45	2.21	2.26	2.05	1.84	14.91		0.059
Chiroptera	Pteropodidae	*Epomophorus gambianus*	1.27	4.30	2.59	2.50	2.54	2.40	2.51	18.11		0.080
Chiroptera	Pteropodidae	*Pteropus alecto*	1.63	7.73	4.99	4.45	4.15	3.99	3.32	30.26		0.672
Chiroptera	Pteropodidae	*Pteropus giganteus*	2.90	8.52	6.69	6.85	6.29	5.28	4.03	40.56	49.02	1.175
Chiroptera	Pteropodidae	*Pteropus poliocephalus*	2.03	9.07	5.41	5.05	5.70	4.60	4.20	36.06	101.98	0.675
Chiroptera	Pteropodidae	*Pteropus pselaphon*	1.44	7.09	4.12	3.80	3.98	3.98	2.92	27.33	67.16	0.500
Chiroptera	Pteropodidae	*Pteropus vampyrus*	2.71	10.37	7.46	6.90	6.58	6.04	4.93	44.97	52.73	0.872
Chiroptera	Pteropodidae	*Rousettus aegyptiacus*	1.01	4.59	2.70	2.69	2.75	2.51	2.16	18.41	84.89	0.125
Chiroptera	Rhinolophidae	*Rhinolophus hipposideros*	0.39	1.55	0.94	0.87	0.82	0.76	0.71	6.04	17.19	0.005
Chiroptera	Vespertilionidae	*Barbastella barbastellus*	0.50	1.63	1.16	1.01	1.01	0.80	0.85	6.96	16.47	0.010
Chiroptera	Vespertilionidae	*Eptesicus serotinus*	0.73	2.05	1.25	1.18	1.14	1.14	1.07	8.54	16.60	0.018
Chiroptera	Vespertilionidae	*Miniopterus schreibersii*	0.63	2.22	1.51	1.52	1.44	1.27	1.20	9.79	18.56	0.013
Chiroptera	Vespertilionidae	*Myotis daubentonii*	0.59	1.91	0.89	0.93	0.92	0.89	0.79	6.92	16.46	0.009
Chiroptera	Vespertilionidae	*Myotis nattereri*	0.53	1.70	0.97	0.92	0.88	0.81	0.75	6.56	27.67	0.008
Chiroptera	Vespertilionidae	*Nyctalus noctula*	0.72	2.63	1.73	1.51	1.35	1.26	1.09	10.29		0.028
Chiroptera	Vespertilionidae	*Plecotus auritus*	0.59	1.68	1.07	1.00	0.95	0.86	0.69	6.84	17.86	0.008
Chiroptera	Vespertilionidae	*Plecotus austriacus*	0.62	2.19	1.26	1.20	1.16	1.03	0.87	8.33	16.80	0.012
Dermoptera	Cynocephalidae	*Cynocephalus volans*	4.86	12.03	9.33	8.92	8.75	8.56	7.37	59.82	123.18	1.300
Dermoptera	Cynocephalidae	*Galeopterus variegatus*	5.08	12.85	9.47	8.54	7.88	7.83	7.23	58.88	123.24	1.300
Eulipotyphla	Erinaceidae	*Echinosorex gymnura*	2.09	8.99	5.72	5.50	4.96	4.86	4.66	36.77	53.86	1.250

Clade	Family	Species	C1	C2	C3	C4	C5	C6	C7	Cervical spine	Tibia	Body weight
Eulipotyphla	Erinaceidae	*Erinaceus europaeus*	2.35	4.33	2.98	2.64	2.51	2.42	2.50	19.73	34.72	0.750
Eulipotyphla	Erinaceidae	*Erinaceus roumanicus*	2.33	4.18	3.37	2.77	2.57	2.56	2.71	20.48	42.18	0.750
Eulipotyphla	Erinaceidae	*Hemiechinus auritus*	2.09	5.13	2.93	3.30	3.11	3.30	3.20	23.06	65.52	0.342
Eulipotyphla	Erinaceidae	*Hylomys suillus*	0.85	2.72	2.02	1.78	1.63	1.49	1.35	11.83	23.35	0.069
Eulipotyphla	Erinaceidae	*Paraechinus aethiopicus*	1.41	3.24	2.44	2.38	2.24	2.03	2.39	16.13	35.07	0.188
Eulipotyphla	Erinaceidae	*Paraechinus micropus*	1.55	3.50	2.87	2.62	2.67	2.80	3.00	19.01	39.41	0.360
Eulipotyphla	Solenodontidae	*Solenodon paradoxus*	1.78	6.68	3.88	3.66	3.13	3.09	3.04	25.24	140.62	1.000
Eulipotyphla	Soricidae	*Blarina brevicauda*	0.40	1.87	1.35	1.29	1.11	1.09	0.92	8.03		0.022
Eulipotyphla	Soricidae	*Crocidura leucodon*	0.24	1.71	1.05	1.01	1.00	0.91	0.85	6.77	12.32	0.011
Eulipotyphla	Soricidae	*Crocidura russula*	0.35	1.73	1.11	0.98	0.82	0.80	0.82	6.61	12.96	0.012
Eulipotyphla	Soricidae	*Neomys fodiens*	0.23	1.70	0.94	0.75	0.71	0.75	0.73	5.80	15.23	0.015
Eulipotyphla	Soricidae	*Sorex araneus*	0.34	1.58	0.94	0.85	0.78	0.75	0.84	6.06	14.00	0.009
Eulipotyphla	Soricidae	*Sorex cinereus*	0.22	1.26	0.70	0.70	0.59	0.56	0.56	4.59	12.06	0.004
Eulipotyphla	Soricidae	*Sorex coronatus*	0.32	1.59	1.01	0.90	0.75	0.74	0.81	6.10	13.20	0.010
Eulipotyphla	Soricidae	*Sorex minutus*	0.24	1.24	0.79	0.79	0.60	0.65	0.65	4.95	10.37	0.007
Eulipotyphla	Soricidae	*Sorex trowbridgii*	0.27	1.40	0.72	0.75	0.70	0.67	0.66	5.17	12.92	0.008
Eulipotyphla	Soricidae	*Suncus etruscus*	0.25	1.23	0.66	0.62	0.59	0.57	0.55	4.47		0.002
Eulipotyphla	Talpidae	*Desmana moschata*	1.22	4.15	2.11	2.03	2.42	2.50	2.40	16.83	40.14	0.220
Eulipotyphla	Talpidae	*Mogera wogura*	0.64	3.45	2.43	2.09	2.15	2.26	2.03	15.05	18.40	0.097
Eulipotyphla	Talpidae	*Talpa europaea*	1.90	2.93	2.12	2.01	2.05	2.21	1.77	14.99	19.44	0.093
Hyracoidea	Procavidae	*Dendrohyrax arboreus*	4.10	12.56	8.01	7.27	6.80	6.93	6.26	51.91	60.85	3.000
Hyracoidea	Procavidae	*Dendrohyrax dorsalis*	5.40	14.45	9.72	9.06	7.23	6.75	6.20	58.81	75.70	3.000
Hyracoidea	Procavidae	*Heterohyrax brucei*	4.57	11.37	7.03	6.77	6.60	6.62	5.74	48.69	58.97	2.457
Hyracoidea	Procavidae	*Procavia capensis*	4.43	12.94	7.23	6.25	5.82	5.56	4.64	46.87	93.25	3.600
Lagomorpha	Leporidae	*Lepus americanus*	2.47	11.99	9.30	8.63	7.60	6.41	6.40	52.80	113.04	1.600
Lagomorpha	Leporidae	*Lepus brachyurus*	3.31	14.54	11.15	9.52	8.99	7.89	5.59	60.99	124.67	2.519
Lagomorpha	Leporidae	*Lepus capensis*	2.64	13.33	9.61	8.66	7.75	6.11	4.76	52.86	101.46	2.358
Lagomorpha	Leporidae	*Lepus europaeus*	5.22	14.69	12.28	10.64	9.38	8.78	7.55	68.52	132.19	4.175
Lagomorpha	Leporidae	*Lepus habessinicus*	3.05	13.90	10.29	9.92	9.01	8.10	6.53	60.80	118.24	2.000

Clade	Family	Species	C1	C2	C3	C4	C5	C6	C7	Cervical spine	Tibia	Body weight
Lagomorpha	Leporidae	*Lepus timidus*	5.55	13.54	10.30	9.70	9.00	7.70	6.36	62.14	139.50	4.175
Lagomorpha	Leporidae	*Lepus whytei*	2.73	12.17	8.98	8.54	8.29	6.94	6.40	54.05	98.49	2.250
Lagomorpha	Leporidae	*Oryctolagus cuniculus*	3.55	8.84	7.18	6.16	5.83	4.87	4.07	40.48	87.41	1.800
Lagomorpha	Leporidae	*Sylvilagus floridanus*	3.00	11.56	7.66	6.77	6.19	6.29	5.06	46.53	94.05	1.150
Lagomorpha	Ochotonidae	*Ochotona curzoniae*	1.01	4.48	3.65	3.61	3.01	2.45	1.94	20.15	30.65	0.140
Lagomorpha	Ochotonidae	*Ochotona roylei*	1.02	4.40	3.26	3.19	3.01	2.67	2.16	19.71	35.57	0.155
Lagomorpha	Ochotonidae	*Ochotona rufescens*	2.28	6.42	4.70	4.45	3.45	3.69	2.36	27.35	40.77	0.260
Macroscelidea	Macrosclidae	*Elephantulus brachyrhynchus*	0.94	2.37	1.69	1.48	1.40	1.07	1.17	10.12	32.72	0.044
Macroscelidea	Macrosclidae	*Elephantulus intufi*	1.12	2.27	1.62	1.31	1.21	1.00	0.99	9.52		0.052
Macroscelidea	Macrosclidae	*Elephantulus rozeti*	0.83	2.02	1.30	1.13	0.92	0.87	0.90	7.96	32.21	0.048
Macroscelidea	Macrosclidae	*Petrodromus tetradactylus*	1.59	4.60	2.85	2.46	2.17	1.96	1.85	17.47	56.00	0.210
Macroscelidea	Macrosclidae	*Rhynchocyon cirnei*	2.56	5.41	3.60	3.27	3.11	2.70	2.94	23.56	68.22	0.370
Macroscelidea	Macrosclidae	*Rhynchocyon petersi*	2.51	6.01	3.25	3.52	3.01	2.86	3.09	24.25	62.27	0.550
Macroscelidea	Macrosclidae	*Rhynchocyon spec.*	2.46	5.71	4.08	3.57	3.21	2.91	2.69	24.63		0.530
Marsupialia	Dasyuridae	*Dasyurus spec.*	1.72	4.24	2.60	2.43	2.10	2.56	2.54	18.19	45.80	0.250
Marsupialia	Dasyuridae	*Dasyurus viverrinus*	3.61	7.93	5.49	4.87	3.97	3.92	3.72	33.51		1.090
Marsupialia	Dasyuridae	*Sarcophilus harrisii*	5.35	14.98	4.99	4.71	4.54	4.53	4.27	43.37	82.11	6.500
Marsupialia	Didelphidae	*Chironectes minimus*	1.70	6.73	3.84	3.87	3.77	3.09	2.60	25.60	84.47	0.700
Marsupialia	Didelphidae	*Didelphis aurita*	1.52	6.63	4.01	3.57	3.39	3.66	3.25	26.03	44.84	0.850
Marsupialia	Didelphidae	*Didelphis marsupialis*	2.70	9.69	6.51	5.94	4.15	5.29	4.23	38.51		1.530
Marsupialia	Didelphidae	*Didelphis virginiana*	3.30	12.48	7.84	6.53	6.13	5.95	5.32	47.53	47.03	3.000
Marsupialia	Didelphidae	*Lutreolina crassicaudata*	1.57	9.38	5.04	4.79	4.32	4.40	4.45	33.95	88.02	0.370
Marsupialia	Didelphidae	*Marmosa spec.*	1.20	3.89	1.83	1.79	1.61	1.71	1.78	13.80	22.36	0.075
Marsupialia	Didelphidae	*Philander opossum*	1.39	8.15	4.80	4.04	3.47	4.14	3.46	29.45	44.96	0.450
Marsupialia	Macropodidae	*Dendrolagus matschiei*	3.55	11.70	6.87	6.65	6.50	6.18	5.72	47.17	50.40	7.200
Marsupialia	Macropodidae	*Macropus eugenii*	3.60	11.84	6.57	6.28	5.84	6.22	6.68	47.03		6.500
Marsupialia	Macropodidae	*Macropus giganteus*	8.03	33.93	25.43	24.06	21.43	19.01	22.10	153.99	508.14	49.500
Marsupialia	Macropodidae	*Macropus rufogriseus*	3.47	14.32	8.56	8.41	8.15	8.25	8.18	59.32	91.75	16.200
Marsupialia	Macropodidae	*Macropus spec.*	4.48	24.28	13.16	12.28	10.77	10.25	11.06	86.28	385.85	39.000

Clade	Family	Species	C1	C2	C3	C4	C5	C6	C7	Cervical spine	Tibia	Body weight
Marsupialia	Macropodidae	*Petrogale penicillata*	3.17	11.56	6.41	5.64	5.66	5.99	6.11	44.54	89.54	6.000
Marsupialia	Macropodidae	*Petrogale spec.*	2.44	10.64	5.95	4.63	4.53	6.00	4.91	39.10	116.69	6.500
Marsupialia	Macropodidae	*Setonix brachyurus*	1.61	7.06	3.75	3.15	2.78	2.49	3.75	24.59	160.46	3.500
Marsupialia	Macropodidae	*Thylogale brunii*	2.30	5.69	2.05	1.97	2.00	2.33	2.50	18.84	227.41	13.000
Marsupialia	Macropodidae	*Wallabia bicolor*	2.60	12.17	6.55	5.72	5.22	5.15	6.55	43.96	92.60	14.625
Marsupialia	Peramelidae	*Echymipera spec.*	1.25	4.76	1.80	1.67	1.73	1.70	1.63	14.54	59.01	1.250
Marsupialia	Peramelidae	*Perameles nasuta*	1.69	7.39	4.00	3.61	3.67	3.64	3.51	27.51	45.26	0.859
Marsupialia	Petauridae	*Dactylopsila trivirgata*	1.52	5.19	2.41	2.36	2.22	2.34	2.60	18.63	68.60	0.318
Marsupialia	Phalangeridae	*Ailurops ursinus*	3.27	9.96	4.76	4.01	4.15	4.44	4.76	35.35	56.24	7.000
Marsupialia	Phalangeridae	*Spilocuscus maculatus*	2.77	9.47	4.93	4.39	4.00	3.65	3.77	32.96	88.39	3.500
Marsupialia	Phalangeridae	*Strigocuscus celebensis*	2.01	8.96	3.76	3.42	3.31	3.73	4.08	29.27	76.36	1.050
Marsupialia	Phalangeridae	*Trichosurus vulpecula*	2.79	9.36	5.23	4.29	4.06	3.72	4.20	33.63	74.96	2.395
Marsupialia	Phascolarctidae	*Phascolarctos cinereus*	3.38	17.11	8.57	7.79	7.01	6.74	7.39	57.97	91.57	9.300
Marsupialia	Potoroidae	*Aepyprymnus rufescens*	2.27	6.67	3.10	2.36	3.25	3.57	2.54	23.76	110.88	3.250
Marsupialia	Potoroidae	*Bettongia penicillata*	3.35	4.96	2.99	2.62	2.70	2.72	2.78	22.12	121.75	1.500
Marsupialia	Pseudocheiridae	*Petauroides volans*	2.04	5.37	2.58	2.40	2.38	2.25	2.25	19.27	50.68	1.350
Marsupialia	Vombatidae	*Lasiorhinus latifrons*	5.10	18.82	8.86	7.73	7.92	9.00	10.96	68.37	80.65	25.500
Monotremata	Ornithorhynchidae	*Ornithorhynchus anatinus*	5.33	11.49	6.37	5.56	5.18	5.41	5.09	44.42	49.52	1.250
Monotremata	Tachyglossidae	*Tachyglossus aculeatus*	3.02	16.73	7.24	6.71	6.60	6.55	6.28	53.11	64.90	3.500
Monotremata	Tachyglossidae	*Zaglossus bruijni*	5.93	23.63	10.95	10.22	10.38	9.92	9.92	80.95		7.500
Perissodactyla	Equidae	*Equus asinus*	33.81	110.50	65.52	67.07	56.90	49.41	32.99	416.20	298.00	165.000
Perissodactyla	Equidae	*Equus burchellii*	35.65	121.38	81.50	69.26	62.84	50.69	34.99	456.31	205.00	280.000
Perissodactyla	Equidae	*Equus caballus*	39.04	122.29	82.11	80.66	74.53	66.85	42.21	507.68	320.44	300.000
Perissodactyla	Equidae	*Equus kiang*	30.84	110.31	74.05	72.59	66.67	55.79	37.37	447.62	310.00	275.000
Perissodactyla	Tapiridae	*Tapirus indicus*	33.57	68.84	33.87	33.39	34.46	35.05	36.21	275.39	253.00	250.000
Perissodactyla	Tapiridae	*Tapirus pinchaque*	19.39	49.15	27.08	29.04	27.91	28.26	28.79	209.62	306.00	148.950
Pholidota	Manidae	*Manis javanica*	4.22	11.20	8.08	7.78	8.21	8.18	9.72	57.39	69.58	8.000
Pholidota	Manidae	*Manis pentadactyla*	4.61	10.81	7.16	6.80	6.79	6.51	6.22	48.90	52.75	2.350
Pholidota	Manidae	*Manis temminckii*	4.66	11.40	7.41	6.68	6.71	7.39	7.64	51.89	85.00	15.000

Clade	Family	Species	C1	C2	C3	C4	C5	C6	C7	Cervical spine	Tibia	Body weight
Pholidota	Manidae	*Manis tricuspis*	2.95	6.30	3.26	3.22	3.22	3.20	3.60	25.75	48.76	4.500
Primates	Aotidae	*Aotus trivirgatus*	2.49	4.52	2.65	2.86	2.55	2.57	2.67	20.31	76.06	0.800
Primates	Atelidae	*Lagothrix lagotricha*	4.69	10.21	5.91	5.87	5.60	5.47	5.87	43.62	157.18	7.650
Primates	Callitrichidae	*Callimico goeldii*	2.25	7.11	4.20	4.12	3.29	3.70	3.73	28.40	75.37	0.555
Primates	Callitrichidae	*Callithrix argentata*	1.83	5.98	3.49	2.89	2.90	2.89	3.25	23.23	58.74	0.343
Primates	Callitrichidae	*Callithrix geoffroyi*	2.27	5.40	3.37	2.97	2.69	2.55	2.19	21.44	60.11	0.342
Primates	Callitrichidae	*Callithrix jacchus*	2.33	6.01	3.52	3.27	2.93	2.88	3.06	24.00	58.30	0.255
Primates	Callitrichidae	*Callithrix pygmaea*	1.18	3.38	1.95	1.65	1.53	1.44	1.37	12.49	34.51	0.124
Primates	Callitrichidae	*Leontopithecus rosalia*	2.48	5.93	3.61	2.98	2.79	2.89	3.69	24.37	71.95	0.655
Primates	Callitrichidae	*Saguinus fuscicollis*	1.59	4.37	2.59	2.42	2.43	2.68	2.73	18.81	44.82	0.457
Primates	Callitrichidae	*Saguinus oedipus*	3.43	5.86	3.18	2.94	3.05	3.05	4.00	25.51		0.446
Primates	Cebidae	*Cebus apella*	5.12	7.41	6.09	5.05	4.70	4.37	5.15	37.89	105.63	2.643
Primates	Cebidae	*Saimiri sciureus*	2.59	5.99	4.49	3.83	3.40	3.69	3.85	27.84	76.49	0.925
Primates	Cercopithecidae	*Cercopithecus cephus*	2.36	6.87	4.55	4.05	4.05	4.02	3.60	29.50	112.39	3.585
Primates	Cercopithecidae	*Cercopithecus diana*	9.52	9.52	6.28	6.22	6.21	5.25	4.61	47.61	136.94	4.550
Primates	Cercopithecidae	*Chlorocebus aethiops*	2.65	7.51	4.44	3.80	3.73	3.81	3.71	29.65	114.94	5.620
Primates	Cercopithecidae	*Macaca mulatta*	2.72	6.31	2.81	2.75	2.62	2.53	2.43	22.17		8.235
Primates	Cercopithecidae	*Macaca nigra*	3.20	9.11	6.47	5.87	5.68	5.56	5.37	41.26		7.965
Primates	Cercopithecidae	*Macaca radiata*	3.75	8.61	3.78	3.63	3.43	3.24	3.14	29.58	113.85	6.755
Primates	Cercopithecidae	*Macaca spec.*	7.04	10.51	8.13	7.11	6.65	5.88	7.18	52.50	177.26	8.500
Primates	Cercopithecidae	*Mandrillus sphinx*	7.56	16.11	10.66	8.75	8.20	7.15	6.74	65.17		23.000
Primates	Cercopithecidae	*Miopithecus talapoin*	1.91	5.08	3.00	2.65	2.68	2.68	2.90	20.90	93.79	1.385
Primates	Cercopithecidae	*Semnopithecus entellus*	7.06	10.15	7.97	7.03	6.36	6.11	6.13	50.81		13.517
Primates	Cheirogaleidae	*Microcebus murinus*	0.86	2.43	1.49	1.45	1.32	1.25	1.22	10.02	19.52	0.065
Primates	Daubentoniidae	*Daubentonia madagascariensis*	4.08	8.86	4.22	3.48	3.66	3.81	4.33	32.44	115.35	2.278
Primates	Galagonidae	*Galago alleni*	1.75	5.40	3.64	2.93	2.91	2.81	3.00	22.44	72.24	0.273
Primates	Galagonidae	*Galago senegalensis*	1.55	4.77	2.78	2.34	2.16	2.13	2.02	17.75	30.29	0.192
Primates	Galagonidae	*Galagoides demidoff*	1.11	3.70	2.40	1.64	1.96	1.90	1.65	14.36	53.15	0.060
Primates	Galagonidae	*Otolemur crassicaudatus*	2.33	7.81	5.24	4.70	3.81	4.18	3.86	31.93	50.37	1.095

Clade	Family	Species	C1	C2	C3	C4	C5	C6	C7	Cervical spine	Tibia	Body weight
Primates	Hominidae	*Gorilla gorilla*	12.84	18.44	10.34	11.32	11.89	13.65	12.60	91.08	251.63	140.000
Primates	Hominidae	*Homo sapiens*	9.62	19.73	10.98	10.75	10.46	9.10	13.54	84.18	375.45	65.000
Primates	Hominidae	*Pongo abelii*	12.12	19.06	11.00	10.00	10.42	11.15	10.56	84.31	241.76	64.500
Primates	Hylobatidae	*Hylobates spec.*	5.20	9.77	7.35	6.86	6.34	5.84	5.54	46.90		7.000
Primates	Indriidae	*Avahi laniger*	2.58	8.65	6.08	5.80	5.24	5.39	5.20	38.94	102.78	1.200
Primates	Lemuridae	*Varecia variegata*	3.17	12.25	8.95	8.02	7.69	8.02	7.32	55.42	55.23	3.670
Primates	Lorisidae	*Arctocebus calabarensis*	1.52	5.58	3.79	3.44	3.37	3.13	3.13	23.96	79.37	0.258
Primates	Lorisidae	*Nycticebus coucang*	2.93	7.69	4.00	3.52	3.68	3.94	4.66	30.42	163.01	0.891
Primates	Lorisidae	*Perodicticus potto*	3.01	7.57	4.93	3.88	4.29	4.45	4.00	32.13	79.87	1.225
Primates	Pitheciidae	*Cacajao calvus*	4.91	10.01	6.57	4.92	5.12	5.43	6.10	43.06	112.51	3.165
Primates	Pitheciidae	*Callicebus moloch*	2.68	5.21	3.37	3.20	3.27	3.37	3.85	24.95	79.99	0.804
Primates	Pitheciidae	*Chiropotes satanas*	2.65	7.15	4.79	4.50	4.52	4.83	4.50	32.94	115.48	2.943
Primates	Pitheciidae	*Pithecia monachus*	2.22	5.92	3.34	2.94	3.16	3.27	3.10	23.95	83.74	1.780
Primates	Pitheciidae	*Pithecia pithecia*	2.85	7.59	5.84	4.74	5.09	5.16	5.57	36.84	120.91	1.480
Primates	Tarsiidae	*Tarsius syrichta*	1.39	4.13	2.11	1.95	1.58	1.59	1.41	14.16		0.119
Proboscidea	Elephantidae	*Elephas maximus*	72.11	79.40	46.21	44.43	37.07	38.49	53.78	371.47	601.15	3178.000
Rodentia	Abrocomidae	*Abrocoma spec.*	1.39	5.16	3.78	3.58	2.95	3.00	3.07	22.93	35.92	0.266
Rodentia	Bathyergidae	*Bathyergus suillus*	3.32	4.04	3.19	2.76	2.83	2.77	3.05	21.97	44.37	1.300
Rodentia	Bathyergidae	*Georychus capensis*	1.82	3.20	1.90	1.91	1.82	1.89	1.82	14.36	19.71	0.181
Rodentia	Bathyergidae	*Heliophobius spec.*	1.65	3.09	2.24	2.23	2.11	2.09	2.13	15.54	26.36	0.089
Rodentia	Capromyidae	*Capromys pilorides*	4.49	9.76	7.31	6.79	6.29	5.85	5.10	45.59	80.25	4.683
Rodentia	Castoridae	*Castor fiber*	8.09	8.06	6.20	5.59	5.42	5.86	6.38	45.58	130.74	25.000
Rodentia	Caviidae	*Dolichotis patagonum*	8.23	20.28	14.09	12.80	11.64	10.80	10.64	88.47	159.45	12.250
Rodentia	Caviidae	*Galea musteloides*	2.05	5.29	3.52	4.00	3.72	3.35	2.71	24.64	51.62	0.338
Rodentia	Caviidae	*Kerodon rupestris*	2.64	7.21	4.46	3.86	4.06	4.40	3.71	30.34	55.27	0.950
Rodentia	Chinchillidae	*Chinchilla chinchilla*	1.83	4.53	2.85	2.58	2.55	2.20	2.58	19.12	68.00	0.800
Rodentia	Chinchillidae	*Chinchilla lanigera*	1.57	4.88	3.31	2.95	2.96	2.79	2.56	21.02	46.61	0.643
Rodentia	Chinchillidae	*Lagidium peruanum*	2.34	6.34	4.34	4.12	3.83	3.50	3.36	27.81	84.22	1.250
Rodentia	Chinchillidae	*Lagostomus maximus*	4.00	7.63	4.63	4.53	4.30	4.22	3.75	33.06	108.27	6.000

Clade	Family	Species	C1	C2	C3	C4	C5	C6	C7	Cervical spine	Tibia	Body weight
Rodentia	Cricetidae	*Arvicola amphibius*	1.35	2.95	1.93	1.75	1.71	2.00	1.88	13.57	26.06	0.120
Rodentia	Cricetidae	*Chionomys nivalis*	0.79	1.89	1.15	1.08	0.81	1.08	0.94	7.74	27.69	0.039
Rodentia	Cricetidae	*Cricetus cricetus*	1.77	3.76	2.82	2.70	2.60	2.65	2.55	18.84	37.07	0.507
Rodentia	Cricetidae	*Dicrostonyx torquatus*	1.11	1.16	0.80	0.87	0.86	0.87	0.81	6.48	20.63	0.085
Rodentia	Cricetidae	*Ellobius talpinus*	0.73	1.69	1.08	1.10	1.10	1.09	0.94	7.73	17.47	0.070
Rodentia	Cricetidae	*Lemmus lemmus*	0.84	1.48	1.00	0.90	0.92	0.88	0.77	6.79	21.12	0.070
Rodentia	Cricetidae	*Microtus arvalis*	0.53	1.49	1.30	1.25	1.20	1.09	0.98	7.84	64.20	0.028
Rodentia	Cricetidae	*Myodes glareolus*	0.53	1.40	0.96	0.94	0.93	0.98	0.73	6.47	24.82	0.021
Rodentia	Cricetidae	*Nectomys squamipes*	1.56	4.51	2.22	2.22	2.04	2.02	1.95	16.52	43.55	0.230
Rodentia	Cricetidae	*Neotoma cinerea*	1.50	3.42	2.43	2.23	1.96	2.62	2.01	16.17	40.22	0.257
Rodentia	Ctenomyidae	*Ctenomys tucumanus*	1.69	4.14	1.74	2.18	2.18	2.46	2.79	17.18		0.300
Rodentia	Cuniculidae	*Cuniculus paca*	6.02	14.17	8.67	7.87	6.72	8.08	7.13	58.66	88.03	9.000
Rodentia	Dasyproctidae	*Dasyprocta leporina*	4.82	11.17	8.01	6.91	6.73	6.45	6.88	50.97	92.96	3.265
Rodentia	Dinomyidae	*Dinomys branickii*	7.38	7.78	4.92	4.61	4.74	5.61	6.58	41.62	101.84	12.250
Rodentia	Echimyidae	*Echimys chrysurus*	2.49	6.54	4.10	3.84	4.00	3.88	3.50	28.35	45.19	0.550
Rodentia	Echimyidae	*Echimys spec.*	1.74	3.97	3.06	3.16	2.86	3.03	2.97	20.79	37.20	0.450
Rodentia	Echimyidae	*Makalata didelphoides*	1.75	3.92	3.09	2.93	2.74	2.14	2.14	18.71	35.52	0.276
Rodentia	Echimyidae	*Myocastor coypus*	5.47	8.60	6.00	5.14	4.86	4.86	4.93	39.84	108.74	7.850
Rodentia	Echimyidae	*Proechimys guyannensis*	2.17	5.86	3.47	3.59	3.29	3.22	2.65	24.25	48.80	0.357
Rodentia	Erethizontidae	*Erethizon dorsatum*	5.54	5.99	5.08	4.56	4.27	4.15	4.08	33.67	101.17	8.600
Rodentia	Gliridae	*Eliomys quercinus*	1.61	2.09	1.36	1.24	1.18	1.11	1.24	9.83	25.45	0.083
Rodentia	Gliridae	*Glis glis*	1.07	2.91	1.86	1.68	1.64	1.55	1.92	12.63	30.53	0.120
Rodentia	Gliridae	*Muscardinus avellanarius*	0.55	1.28	0.78	0.60	0.59	0.62	0.69	5.11	17.82	0.027
Rodentia	Hystricidae	*Hystrix brachyurus*	4.73	10.44	6.38	5.31	4.81	5.67	6.13	43.47	65.38	8.000
Rodentia	Hystricidae	*Hystrix cristata*	4.13	13.87	5.77	5.27	5.58	5.80	5.59	46.01	79.06	20.000
Rodentia	Hystricidae	*Hystrix indica*	9.25	21.12	10.39	10.78	9.93	9.14	9.73	80.34	104.44	20.000
Rodentia	Muridae	*Apodemus sylvaticus*	0.64	1.31	1.06	0.98	0.83	0.82	1.07	6.71	42.74	0.023
Rodentia	Muridae	*Bandicota bengalensis*	1.52	4.75	3.20	2.82	2.56	1.85	2.83	19.53	35.40	0.550
Rodentia	Muridae	*Gerbillus latastei*	0.75	1.77	0.88	0.99	0.86	0.79	0.81	6.85	26.01	0.036

Clade	Family	Species	C1	C2	C3	C4	C5	C6	C7	Cervical spine	Tibia	Body weight
Rodentia	Muridae	*Hydromys chrysogaster*	1.64	5.33	3.94	3.74	3.71	3.94	3.97	26.27	75.94	0.850
Rodentia	Muridae	*Lophiomys imhausi*	2.48	5.47	3.51	3.27	3.50	3.55	3.47	25.23	46.95	0.755
Rodentia	Muridae	*Rattus norvegicus*	1.36	2.86	1.80	1.62	1.71	1.67	1.79	12.81		0.300
Rodentia	Muridae	*Tatera indica*	1.48	2.43	1.88	2.03	1.94	1.91	2.02	13.69	40.02	0.147
Rodentia	Nesomyidae	*Cricetomys emini*	3.00	6.43	5.25	5.10	4.90	5.40	5.60	35.68	72.85	1.300
Rodentia	Octodontidae	*Octodon degus*	1.45	3.28	2.39	1.93	1.91	1.74	1.55	14.25	33.59	0.235
Rodentia	Pedetidae	*Pedetes capensis*	3.50	6.09	3.89	3.47	3.33	3.64	3.71	27.61	130.61	3.500
Rodentia	Sciuridae	*Atlantoxerus getulus*	1.45	3.14	2.06	1.93	1.87	1.83	1.79	14.07	43.97	0.400
Rodentia	Sciuridae	*Callosciurus prevostii*	1.95	4.68	3.18	2.81	2.67	2.39	2.50	20.18		0.400
Rodentia	Sciuridae	*Callospermophilus lateralis*	1.58	3.34	1.86	1.81	1.70	1.74	1.80	13.83	38.46	0.158
Rodentia	Sciuridae	*Cynomys ludovicianus*	2.17	4.59	2.27	2.10	2.09	2.27	2.40	17.89	39.46	1.125
Rodentia	Sciuridae	*Marmota marmota*	1.81	6.92	2.67	2.33	2.31	2.21	2.80	21.05	50.84	3.500
Rodentia	Sciuridae	*Petaurista petaurista*	2.23	6.73	4.30	3.75	3.53	3.50	4.45	28.49	102.63	1.750
Rodentia	Sciuridae	*Petinomys setosus*	1.76	3.83	2.32	2.07	2.12	2.16	2.20	16.46	59.99	0.040
Rodentia	Sciuridae	*Ratufa affinis*	2.26	7.19	4.73	4.51	4.22	4.26	4.30	31.47	45.55	1.188
Rodentia	Sciuridae	*Sciurus vulgaris*	1.96	4.49	3.07	3.11	2.81	2.99	2.89	21.32	56.98	0.600
Rodentia	Sciuridae	*Spermophilus citellus*	1.38	3.59	2.40	2.37	2.20	2.20	2.19	16.32	34.69	0.217
Rodentia	Sciuridae	*Tamias sibiricus*	0.99	2.00	1.26	1.12	1.08	1.13	1.14	8.72	30.11	0.085
Rodentia	Sciuridae	*Xerus inauris*	1.84	4.33	2.71	2.64	2.40	2.10	2.09	18.11	52.73	0.588
Rodentia	Spalacidae	*Rhizomys pruinosus*	5.25	4.69	3.57	3.12	3.09	3.40	3.43	26.53	46.48	1.750
Rodentia	Thryonomyidae	*Thryonomys swinderianus*	3.83	8.27	5.69	5.49	4.76	4.98	4.84	37.86	67.94	6.600
Scandentia	Tupaidae	*Tupaia belangeri*	1.17	3.71	2.09	1.93	1.75	1.88	1.91	14.44	30.40	0.200
Scandentia	Tupaidae	*Tupaia javanica*	1.03	3.97	2.34	2.08	2.05	1.90	1.85	15.22		0.200
Scandentia	Tupaidae	*Tupaia minor*	0.83	2.58	1.41	1.21	1.14	1.21	1.30	9.68	29.95	0.059
Scandentia	Tupaidae	*Tupaia tana*	1.55	4.38	2.91	2.71	2.64	2.63	2.45	19.27	48.42	0.198
Sirenia	Dugongidae	*Dugong dugon*	20.57	18.09	9.28	7.92	7.41	8.86	13.35	85.49		360.000
Tubulidenta	Orycteropodidae	*Orycteropus afer*	7.47	22.99	12.57	13.14	13.34	14.37	15.02	98.88	122.82	60.000
Xenarthra	Cyclopedidae	*Cyclopes didactylus*	1.34	3.26	2.17	2.02	2.22	2.15	2.16	15.32	30.41	0.266
Xenarthra	Dasypodidae	*Cabassous unicinctus*	6.53	10.19	7.25	6.42	6.38	7.06	8.17	52.00	59.97	3.500

Clade	Family	Species	C1	C2	C3	C4	C5	C6	C7	Cervical spine	Tibia	Body weight
Xenarthra	Dasypodidae	*Chaetophractus vellerosus*	3.16	7.42	3.14	2.93	2.65	3.48	5.23	28.01	33.99	0.840
Xenarthra	Dasypodidae	*Chlamyphorus truncatus*	1.45	3.72	1.22	0.82	0.99	1.31	1.61	11.12	18.81	0.044
Xenarthra	Dasypodidae	*Dasypus novemcinctus*	4.57	7.50	5.49	5.86	5.52	5.95	6.32	41.20	61.72	5.500
Xenarthra	Dasypodidae	*Priodontes maximus*	11.78	29.25	12.89	10.53	11.00	13.23	17.99	106.67	134.84	33.000
Xenarthra	Dasypodidae	*Tolypeutes matacus*	2.66	8.41	3.26	2.70	2.33	3.35	4.64	27.35	49.21	1.500
Xenarthra	Dasypodidae	*Tolypeutes tricinctus*	2.79	7.79	2.89	3.10	3.05	2.91	4.57	27.10	51.52	1.200
Xenarthra	Myrmecophagidae	*Myrmecophaga tridactyla*	15.08	45.22	29.61	28.54	28.77	28.99	27.33	203.54	188.87	28.500
Xenarthra	Myrmecophagidae	*Tamandua tetradactyla*	4.99	11.98	8.08	7.72	8.80	8.94	7.98	58.46	76.60	4.500

Table S4 Scaling analysis for log cervical spine length against log body weight for mammals in general, for the main mammalian clades, and at the (super)familial level.

	n	slope[a]	slope St.Error	intercept	*F* statistics[b]	AIC
Mammalia	352	0.3**	0.01	3.44	821.39***	118.47
Carnivora	56	0.26*	0.02	3.98	137.1***	3.32
Cetartiodactyla	57	0.25*	0.03	4.04	60.86***	41.46
Marsupialia	32	0.26	0.04	3.26	44.6***	33.42
Primates	43	0.27	0.02	3.32	153.8***	-4.21
Rodentia	63	0.28	0.02	3.12	207.3***	7.4
Bovidae	29	0.23	0.04	4.37	29.29***	19.39
Caviomorpha	19	0.27	0.03	3.35	68.2***	-1.33
Cercopithecidae	10	0.36	0.13	2.91	8.34*	12.74
Felidae	9	0.36	0.06	3.64	34.63***	9.98
Leporidae	9	0.23	0.09	3.78	5.72*	-7.98
Macropodidae+Potoroidae	12	0.47	0.11	2.72	17.29**	20.15
Muroidea	19	0.38	0.03	3.24	151.95***	3.74
Mustelidae	13	0.22**	0.03	3.95	76.55***	0.62
Platyrrhini	7	0.26	0.04	3.31	41.83***	0.96
Pteropodidae	9	0.34	0.04	3.66	92.96***	-0.55
Sciuromorpha	15	0.14***	0.03	2.83	21.26***	7.76
Soricidae	10	0.23	0.03	2.87	52.86***	-18.63

[a] including test for allometry (i.e., significant difference from isometric slope=0.33)

[b] including test for the significance of the regression

n: number of species

AIC: Akaike Information Criterion

Significance levels are: *p<0.05; **p<0.01; ***p<0.001 (corrected for multiple testing).

Table S5 Scaling analysis for log cervical spine length and individual vertebral lengths against log tibial length for mammals in general.

	n	slope[a]	slope St.Error	Intercept	*F* statistics[b]	AIC
C1	313	0.79***	0.05	-2.19	225.59***	452.44
C2	313	0.68***	0.05	-0.59	220.06***	351.78
C3	313	0.68***	0.05	-1.2	191.11***	395.15
C4	313	0.68***	0.05	-1.29	186***	403.37
C5	313	0.7***	0.05	-1.4	194.01***	407.77
C6	313	0.71***	0.05	-1.42	195.24***	416.05
C7	313	0.75***	0.05	-1.64	254.72***	382.64
cervical spine	313	0.71***	0.05	0.65	226.07***	369.57

Footnotes: Articular length (longest distance between proximal and distal articular surfaces) of the tibia was measured in those collections specimens in which it was available with the axial skeleton (313 out of 467) as an alternative proxy for body size. As the results of the regressions are mostly consistent with those on log body weight, more detailed analysis of mammalian sub-clades are not shown. Due to their lack of hind limbs, the fully aquatic mammals (cetaceans, dugong) could not be included in these regressions on tibial length. The main difference is that the positive allometry of the atlas (C1) was not detected.

[a] including test for allometry (i.e., significant difference from isometric slope=1)
[b] including test for the significance of the regression
n: number of species
AIC: Akaike Information Criterion
Significance levels are: *p<0.05; **p<0.01; ***p<0.001 (corrected for multiple testing).

Table S6 Scaling analysis for log cervical vertebral length against log body weight for C1 to C7 in mammals in general, the main mammalian clades, and on the (super)familial level.

	vertebra	slope[a]	slope St.Error	intercept	*F* statistics[b]	AIC
Mammalia	C1	0,35*	0.01	0.95	1330,97***	128.03
Mammalia	C2	0,29***	0.01	2.09	726,16***	119.08
Mammalia	C3	0,28***	0.01	1.49	526,44***	239.55
Mammalia	C4	0,28***	0.01	1.4	504,32***	247.67
Mammalia	C5	0,28***	0.01	1.35	523,2***	243.14
Mammalia	C6	0,29**	0.01	1.36	582,53***	231.96
Mammalia	C7	0,3**	0.01	1.35	801,34***	168.91
Carnivora	C1	0,34	0.02	1.14	183,31***	16.59
Carnivora	C2	0,26**	0.02	2.52	169,74***	-9.91
Carnivora	C3	0,26*	0.03	2.08	99,72***	16.61
Carnivora	C4	0,25*	0.03	2.08	86,09***	22.13
Carnivora	C5	0,24*	0.03	2.06	75,58***	30.7
Carnivora	C6	0,26*	0.03	2	104,91***	17.92
Carnivora	C7	0,26*	0.02	1.88	132,99***	5.57
Cetartiodactyla	C1	0,36	0.03	1.39	162,98***	25.27
Cetartiodactyla	C2	0,22**	0.03	2.57	42,11***	49.52
Cetartiodactyla	C3	0,21**	0.04	2.29	30,66***	59.74
Cetartiodactyla	C4	0,2**	0.04	2.3	30,12***	58.8
Cetartiodactyla	C5	0,21**	0.04	2.22	30,66***	61.85
Cetartiodactyla	C6	0,22*	0.04	2.09	28,89***	71.94
Cetartiodactyla	C7	0,26	0.04	1.8	47,85***	56.66
Marsupialia	C1	0,24*	0.03	0.7	53,56***	22.3
Marsupialia	C2	0,26	0.04	1.96	53,01***	28.04
Marsupialia	C3	0,26	0.05	1.32	29,22***	46.02
Marsupialia	C4	0,25	0.05	1.22	26,8***	47.24
Marsupialia	C5	0,26	0.04	1.16	37,67***	39.39
Marsupialia	C6	0,25	0.04	1.2	35,74***	38.36
Marsupialia	C7	0,28	0.04	1.18	45,16***	37.53
Primates	C1	0,31	0.02	0.95	164,9***	28.61
Primates	C2	0,26**	0.02	1.9	163,78***	-17.14
Primates	C3	0,24**	0.02	1.4	95,97***	12.65
Primates	C4	0,26*	0.02	1.29	122,81***	5.84
Primates	C5	0,28	0.02	1.25	132,25***	2.79
Primates	C6	0,29	0.03	1.25	128,42***	2.58
Primates	C7	0,3	0.03	1.25	105,93***	14.84
Rodentia	C1	0,33	0.02	0.89	331,09***	10.84
Rodentia	C2	0,28	0.02	1.6	166,65***	18.95
Rodentia	C3	0,28	0.02	1.18	156,03***	26.01
Rodentia	C4	0,26*	0.02	1.1	131,46***	28.75
Rodentia	C5	0,27*	0.02	1.05	144,31***	23.77
Rodentia	C6	0,28	0.02	1.08	165,7***	25.78
Rodentia	C7	0,3	0.02	1.11	201,55***	19.77

	vertebra	slope[a]	slope St.Error	intercept	*F* statistics[b]	AIC
Bovidae	C1	0.39***	0.05	1.52	59.07***	15.41
Bovidae	C2	0.26***	0.04	2.73	49.54***	13.14
Bovidae	C3	0.18***	0.05	2.74	14.9***	25.23
Bovidae	C4	0.19***	0.04	2.65	17.37***	22.93
Bovidae	C5	0.2***	0.05	2.49	18.7***	25.16
Bovidae	C6	0.19**	0.06	2.3	8.98**	29.07
Bovidae	C7	0.2***	0.05	1.94	18.43***	24.19
Caviomorpha	C1	0.38***	0.02	0.97	255.06***	-13.54
Caviomorpha	C2	0.26***	0.04	1.86	47.82***	4.28
Caviomorpha	C3	0.27***	0.04	1.43	37.58***	9.19
Caviomorpha	C4	0.24***	0.04	1.39	33.87***	7.35
Caviomorpha	C5	0.24***	0.04	1.33	41.04***	3.6
Caviomorpha	C6	0.27***	0.04	1.32	51.82***	3.42
Caviomorpha	C7	0.27***	0.04	1.29	58.56***	-0.18
Cercopithecidae	C1	0.47	0.21	0.53	4.96	20.92
Cercopithecidae	C2	0.35**	0.08	1.48	19.52*	5.44
Cercopithecidae	C3	0.41*	0.15	0.91	7.25*	15.57
Cercopithecidae	C4	0.39*	0.14	0.84	7.53*	14.44
Cercopithecidae	C5	0.35*	0.14	0.88	5.92*	14.64
Cercopithecidae	C6	0.31*	0.13	0.89	5.86*	12.99
Cercopithecidae	C7	0.3	0.14	0.89	4.77	14.24
Felidae	C1	0.47***	0.05	0.71	103.73***	6.3
Felidae	C2	0.2***	0.02	1.38	86.72***	-25.56
Felidae	C3	0.36**	0.07	1.75	25.08**	12.43
Felidae	C4	0.34**	0.08	1.71	19.58**	13.28
Felidae	C5	0.32*	0.1	1.69	9.75*	17.47
Felidae	C6	0.35**	0.08	1.59	17.03**	14.68
Felidae	C7	0.34***	0.06	1.56	32.13***	9.9
Leporidae	C1	0.53*	0.17	0.78	10.39*	5.58
Leporidae	C2	0.08	0.09	2.39	0.79	-7.77
Leporidae	C3	0.2	0.09	2.03	4.6	-7.74
Leporidae	C4	0.2	0.1	1.92	3.68	-6.51
Leporidae	C5	0.21	0.1	1.84	4.62	-7.59
Leporidae	C6	0.26	0.13	1.72	4.15	2.2
Leporidae	C7	0.23	0.15	1.56	2.48	4.13
Macropodid.+Potoroid.	C1	0.25*	0.1	0.6	6.42*	17.2
Macropodid.+Potoroid.	C2	0.47***	0.09	1.38	25.98***	16
Macropodid.+Potoroid.	C3	0.51**	0.14	0.7	13.05**	24.33
Macropodid.+Potoroid.	C4	0.55**	0.14	0.49	15.27**	24.42
Macropodid.+Potoroid.	C5	0.49**	0.13	0.6	13.43**	23.39
Macropodid.+Potoroid.	C6	0.46**	0.12	0.69	13.7**	21.95
Macropodid.+Potoroid.	C7	0.51**	0.12	0.63	18.06**	20.99
Muroidea	C1	0.39***	0.04	1.02	108.11***	-1.69
Muroidea	C2	0.34***	0.03	1.67	135.31***	-5.24
Muroidea	C3	0.37***	0.03	1.4	220.62***	-15.54
Muroidea	C4	0.36***	0.04	1.22	92.71***	10.02

	vertebra	slope[a]	slope St.Error	intercept	*F* statistics[b]	AIC
Muroidea	C5	0.38***	0.04	1.21	115.85***	8.29
Muroidea	C6	0.39***	0.04	1.24	84.58***	13.86
Muroidea	C7	0.42***	0.04	1.28	106.87***	12.66
Mustelidae	C1	0.29***	0.02	1.07	167.52***	-1.77
Mustelidae	C2	0.24***	0.03	2.41	55.42***	-3.38
Mustelidae	C3	0.21***	0.03	2.08	68.08***	0.51
Mustelidae	C4	0.2***	0.03	2.06	51.08***	3.21
Mustelidae	C5	0.21***	0.03	2.04	45.21***	5.22
Mustelidae	C6	0.22***	0.03	2.01	63.96***	2.09
Mustelidae	C7	0.24***	0.02	1.97	109.46***	-2
Platyrrhini	C1	0.28***	0.06	1	24.43***	12.11
Platyrrhini	C2	0.21***	0.04	1.84	26.45***	1.64
Platyrrhini	C3	0.25***	0.05	1.39	26.9***	7.13
Platyrrhini	C4	0.25***	0.04	1.27	36.81***	2.2
Platyrrhini	C5	0.27***	0.04	1.24	53.69***	-0.79
Platyrrhini	C6	0.28***	0.04	1.25	49.84***	1.08
Platyrrhini	C7	0.29***	0.05	1.32	30.13***	9.73
Pteropodidae	C1	0.39***	0.07	0.86	31.5***	8.83
Pteropodidae	C2	0.34***	0.03	2.22	92.85***	-0.74
Pteropodidae	C3	0.36***	0.04	1.83	83.08***	1.14
Pteropodidae	C4	0.36***	0.04	1.78	79.64***	1.47
Pteropodidae	C5	0.35***	0.04	1.75	73.15***	1.36
Pteropodidae	C6	0.33***	0.03	1.64	104.78***	-1.79
Pteropodidae	C7	0.27***	0.05	1.41	31.63***	3.7
Sciuromorpha	C1	0.19**	0.05	0.67	14.16**	15.01
Sciuromorpha	C2	0.22***	0.03	1.51	56.42***	5.26
Sciuromorpha	C3	0.17**	0.05	0.96	12.86**	11.8
Sciuromorpha	C4	0.27**	0.06	1.04	17.46**	21
Sciuromorpha	C5	0.15**	0.05	0.78	9.37**	14.12
Sciuromorpha	C6	0.1*	0.04	0.68	7.27*	12.58
Sciuromorpha	C7	0.15***	0	0.94	6308.87***	1.53
Soricidae	C1	0.16***	0.09	-0.49	3.14	5.64
Soricidae	C2	0.2***	0.02	1.38	83.02***	-25.56
Soricidae	C3	0.32***	0.04	1.44	62.52***	-11
Soricidae	C4	0.26***	0.05	1.1	30.11***	-10.49
Soricidae	C5	0.25**	0.06	0.93	17.88**	-6
Soricidae	C6	0.25***	0.04	0.92	35.6***	-12.47
Soricidae	C7	0.24***	0.04	0.83	38.81***	-13.97

[a] including test for allometry (i.e., significant difference from isometric slope=0.33)

[b] including test for the significance of the regression

AIC: Akaike Information Criterion

Significance levels are: *p<0.05; **p<0.01; ***p<0.001 (corrected for multiple testing).

Table S7 Loadings of the phylogenetic informed PCA of vertebral lengths, overall cervical spine length, and body weight (all log-transformed).

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
C1	-0.906	0.328	0.263	-0.052	-0.009	-0.004	0.001	0	0.005
C2	-0.971	-0.027	-0.008	0.187	-0.146	-0.005	0.006	0	0.007
C3	-0.98	-0.148	0.026	0.05	0.074	0.068	-0.066	0.026	0.007
C4	-0.981	-0.16	0.021	0.029	0.073	0.026	0.032	-0.065	0.005
C5	-0.981	-0.157	0	0	0.064	-0.038	0.066	0.047	0.005
C6	-0.981	-0.126	-0.034	-0.074	-0.009	-0.113	-0.049	-0.013	0.003
C7	-0.97	-0.038	-0.097	-0.19	-0.095	0.062	0.012	0.002	0.005
body weight	-0.871	0.445	-0.194	0.04	0.06	-0.004	-0.001	-0.001	0.001
cervical spine	-0.998	-0.041	0.019	0.01	-0.01	0.008	0	0.003	-0.037
standard deviation	2.882	0.631	0.345	0.29	0.222	0.153	0.111	0.086	0.04
proportion of variance	0.923	0.044	0.013	0.009	0.005	0.003	0.001	0.001	0
cumulative proportion	0.923	0.967	0.98	0.99	0.995	0.998	0.999	1	1
lambda:	0.8514								

Time-tree in Nexus format

END;

BEGIN TREES;

Title 'Trees_complete';

ID 015659e60e803;

LINK Taxa = Taxa;

TRANSLATE

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[3] 4 Ailurops_ursinus,
[4] 5 Ailurus_fulgens,
[5] 6 Alces_alces,
[6] 7 Antilocapra_americana,
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END;

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		TITLE AUTO;
		tell ProjectCoordinator;
		timeSaved 1475049277065;
		getEmployee #mesquite.minimal.ManageTaxa.ManageTaxa;
		tell It;
			setID 0 1259692222408007471;
			tell It;
				setDefaultOrder  183 78 337 335 49 134 103 38 268 195 70 276
201 64 217 272 136 142 93 196 160 166 338 106 8 107 289 259 255 266 264 262 263 265 216
219 89 29 28 114 115 120 182 212 269 132 133 131 248 247 293 186 185 202 325 258 56 245
309 26 208 198 15 16 57 175 172 27 295 58 283 67 219 348 171 293 325 326 281 299 300 340
18 204 321 320 319 187 152 168 298 177 176 305 6 329 316 315 314 303 226 203 146 153
163 84 83 82 85 173 2 1 74 73 279 280 278 169 282 62 41 64 71 70 166 192 104 224 241 167
61 308 3 68 115 59 302 100 101 110 242 65 197 243 7 188 190 189 60 42 94 170 127 128 96
186 183 270 90 330 205 266 76 235 229 231 230 232 233 234 121 191 40 323 39 80 252 253
251 250 344 345 342 343 122 123 178 249 21 22 23 24 318 221 37 36 48 272 304 199 156 248
19 95 134 225 46 44 47 45 180 202 161 162 296 117 35 207 9 206 160 25 276 236 237 238
174 103 99 111 125 352 317 228 50 75 30 277 118 81 4 5 210 129 328 274 213 349 212 313
339 338 142 331 322 54 52 256 255 157 158 240 93 33 291 79 66 301 34 179 136 116 150 147
149 151 148 78 53 124 196 223 126 145 209 312 311 310 154 112 155 260 259 120 269 327
214 244 306 347 0 12 13 11 10 14 220 335 98 333 17 144 143 227 351 20 297 222 86 87 239
193 140 307 164 341 290 289 107 109 139 108 137 138 332 284 287 286 285 97 56 273 89 91
72 43 32 31 346 217 350 51;
				attachments ;
			endTell;
		endTell;
		getWindow;
		tell It;
			suppress;
			setResourcesState false false 198;
			setPopoutState 300;
			setExplanationSize 0;
```

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					setAnnotationSize 0;
					setFontIncAnnot 0;
					setFontIncExp 0;
					setSize 1920 1119;
					setLocation -306 -1177;
					setFont SanSerif;
					setFontSize 10;
					getToolPalette;
					tell It;
					endTell;
					desuppress;
				endTell;
				getEmployee  #mesquite.minimal.ManageTaxa.ManageTaxa;
				tell It;
					showTaxa                                    #1259692222408007471
#mesquite.lists.TaxonList.TaxonList;
					tell It;
						setTaxa #1259692222408007471;
						getWindow;
						tell It;
							newAssistant
#mesquite.lists.TaxonListCurrPartition.TaxonListCurrPartition;
							setExplanationSize 30;
							setAnnotationSize 20;
							setFontIncAnnot 0;
							setFontIncExp 0;
							setSize 1722 1047;
							setLocation -306 -1177;
							setFont SanSerif;
							setFontSize 10;
							getToolPalette;
							tell It;
								setTool
mesquite.lists.TaxonList.TaxonListWindow.sort;
							endTell;
```

```
					endTell;
					showWindow;
					getEmployee #mesquite.lists.ColorTaxon.ColorTaxon;
					tell It;
						setColor Red;
						removeColor off;
					endTell;
					getEmployee
#mesquite.lists.TaxonListAnnotPanel.TaxonListAnnotPanel;
					tell It;
						togglePanel off;
					endTell;
				endTell;
			endTell;
			getEmployee
#mesquite.trees.BasicTreeWindowCoord.BasicTreeWindowCoord;
			tell It;
				makeTreeWindow                              #1259692222408007471
#mesquite.trees.BasicTreeWindowMaker.BasicTreeWindowMaker;
				tell It;
					suppressEPCResponse;
					setTreeSource  #mesquite.trees.StoredTrees.StoredTrees;
					tell It;
						setTreeBlock 1;
						setTreeBlockID 015659e60e803;
						toggleUseWeights off;
					endTell;
					setAssignedID 1247.1470292120272.7080462321222709515;
					getTreeWindow;
					tell It;
						setExplanationSize 30;
						setAnnotationSize 20;
						setFontIncAnnot 0;
						setFontIncExp 0;
						setSize 1722 1047;
```

```
setLocation -306 -1177;
setFont SanSerif;
setFontSize 10;
getToolPalette;
tell It;
	setTool
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endTell;
setActive;
getTreeDrawCoordinator
#mesquite.trees.BasicTreeDrawCoordinator.BasicTreeDrawCoordinator;
tell It;
	suppress;
	setTreeDrawer
#mesquite.ornamental.CircularTree.CircularTree;
	tell It;
		setEdgeWidth 6;
		getEmployee
#mesquite.ornamental.NodeLocsCircular.NodeLocsCircular;
		tell It;
			branchLengthsToggle on;
			toggleScale on;
		endTell;
	endTell;
	setBackground White;
	setBranchColor Black;
	showNodeNumbers off;
	showBranchColors on;
	labelBranchLengths off;
	centerBrLenLabels on;
	showBrLensUnspecified on;
	showBrLenLabelsOnTerminals on;
	setBrLenLabelColor 0 0 255;
	setNumBrLenDecimals 6;
	desuppress;
```

```
getEmployee
#mesquite.trees.BasicDrawTaxonNames.BasicDrawTaxonNames;
tell It;
setColor Black;
toggleColorPartition off;
toggleColorAssigned on;
toggleShadePartition off;
toggleShowFootnotes on;
toggleNodeLabels on;
toggleCenterNodeNames off;
toggleShowNames on;
namesAngle ?;
endTell;
endTell;
setTreeNumber 1;
setDrawingSizeMode 0;
toggleLegendFloat on;
scale -1;
toggleTextOnTree off;
togglePrintName on;
showWindow;
endTell;
desuppressEPCResponse;
getEmployee #mesquite.trees.ColorBranches.ColorBranches;
tell It;
setColor Red;
removeColor off;
endTell;
getEmployee #mesquite.ornamental.BranchNotes.BranchNotes;
tell It;
setAlwaysOn off;
endTell;
getEmployee
#mesquite.ornamental.ColorTreeByPartition.ColorTreeByPartition;
tell It;
```

```
                    colorByPartition off;
                endTell;
                getEmployee
#mesquite.ornamental.DrawTreeAssocDoubles.DrawTreeAssocDoubles;
                tell It;
                    setOn on;
                    setDigits 4;
                    writeAsPercentage off;
                    toggleCentred off;
                    toggleHorizontal on;
                    toggleWhiteEdges on;
                    toggleShowOnTerminals on;
                    setFontSize 10;
                    setOffset 0  0;
                endTell;
                getEmployee
#mesquite.ornamental.DrawTreeAssocStrings.DrawTreeAssocStrings;
                tell It;
                    setOn on;
                    toggleCentred on;
                    toggleHorizontal on;
                    setFontSize 10;
                    setOffset 0  0;
                    toggleShowOnTerminals on;
                endTell;
                getEmployee #mesquite.trees.TreeInfoValues.TreeInfoValues;
                tell It;
                    panelOpen false;
                endTell;
            endTell;
        endTell;
        endTell;
end;
```

Supplementary Material of Chapter 3

Musculoskeletal networks reveal topological disparity in mammalian neck evolution

Patrick Arnold, Borja Esteve-Altava, Martin S. Fischer

Musculoskeletal networks reveal topological disparity in mammalian neck evolution

Patrick Arnold*, Borja Esteve-Altava, Martin S. Fischer

Additional file AF1_results

*author of correspondence: patrick_arnold@eva.mpg.de

Phylogenetic Analysis

Table A1 Abouheif's test results

	Observed	Standard deviation	p-value
N	0.3716330	3.6217111	0.0009990
K	0.4205506	4.0252417	0.0009990
D	0.3664639	3.9855066	0.0009990
C	0.1329669	1.3724624	0.1878122
L	0.1715729	1.7239277	0.0899101
H	0.3588361	3.5817741	0.0009990
M	0.0136676	0.1738902	0.8761239
P	0.3542345	3.6404221	0.0009990

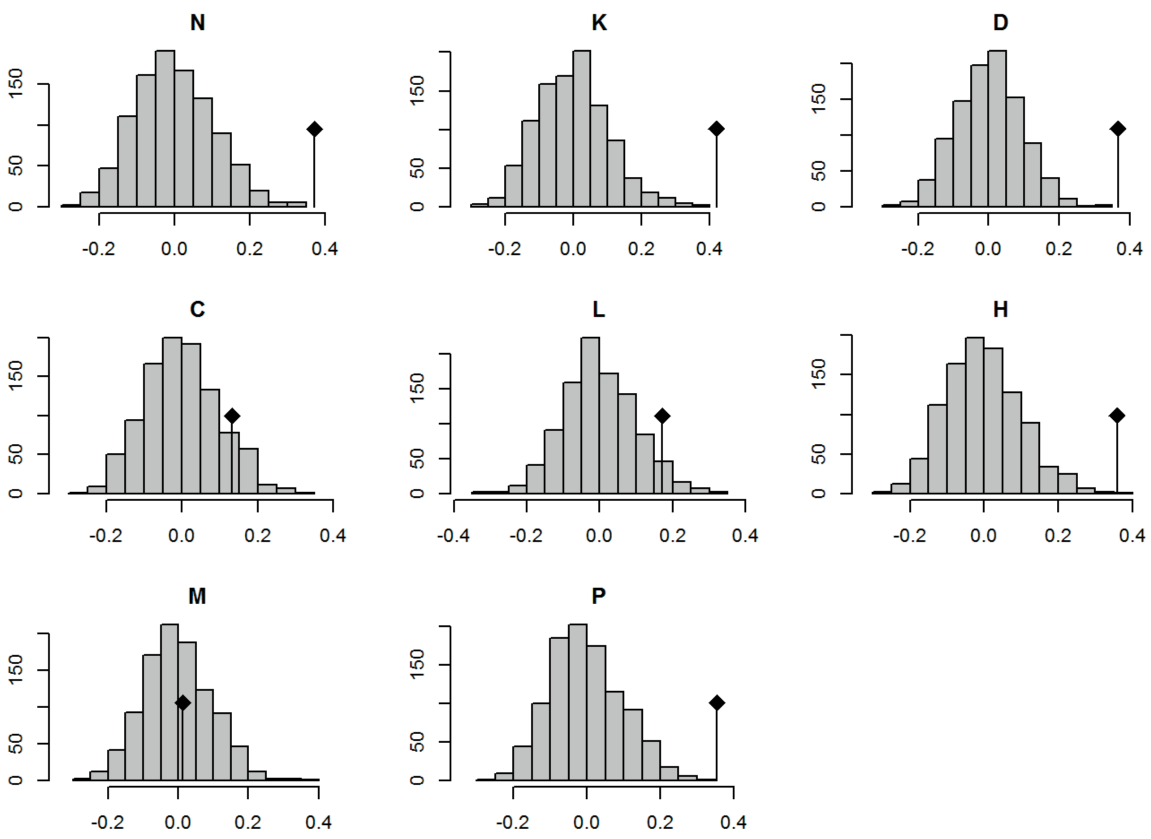

Figure A1 Abouheif's test results (graphically)

Table A2 Blomberg's test results

	K	Observed variance	Expected variance	p-value
N	0.9949704	1.0183979	1.6611474	0.0009990
K	0.8787754	15.1372167	26.6005918	0.0009990
D	1.4785578	0.0000004	0.0000007	0.0009990
C	0.5590563	0.0000347	0.0000364	0.3466533
L	0.7615715	0.0000943	0.0001109	0.0719281
H	1.1083660	0.0000750	0.0001315	0.0009990
M	0.5257506	0.0118682	0.0124085	0.3336663
P	0.6403939	0.0000112	0.0000143	0.0119880

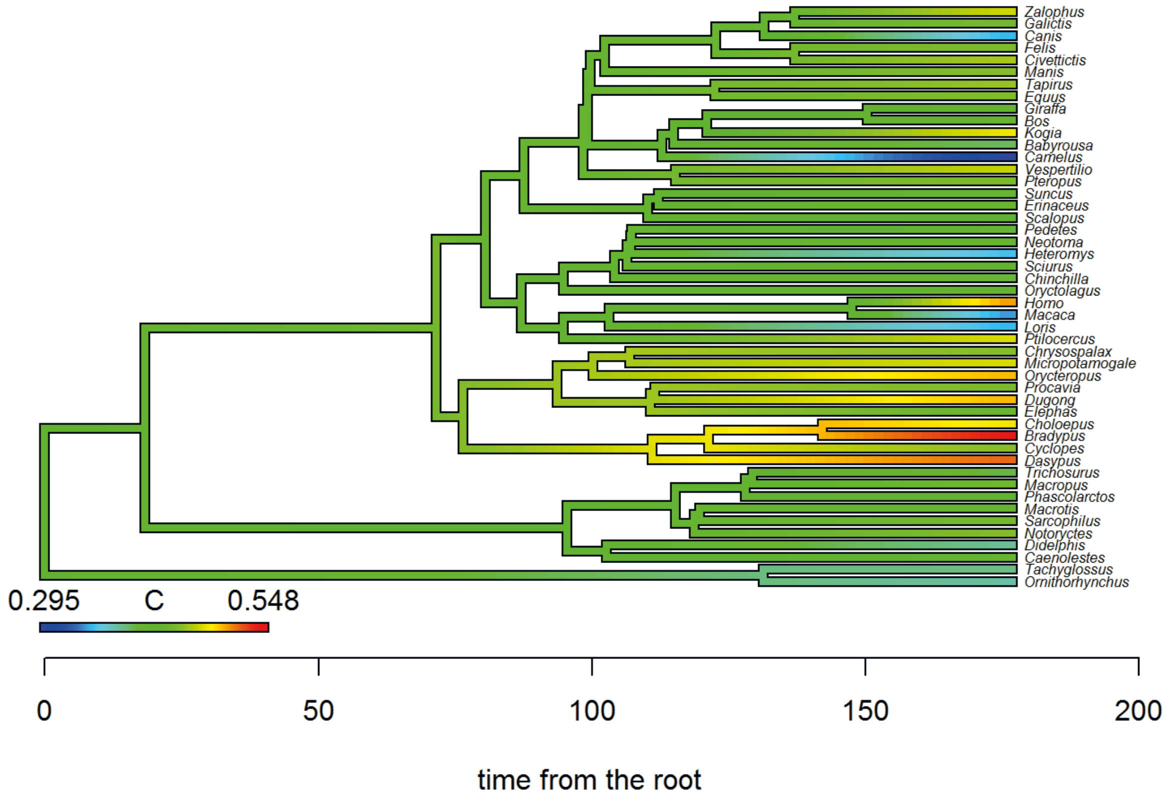

Figure A2 Network average clustering coefficient (C) mapped on the phylogeny

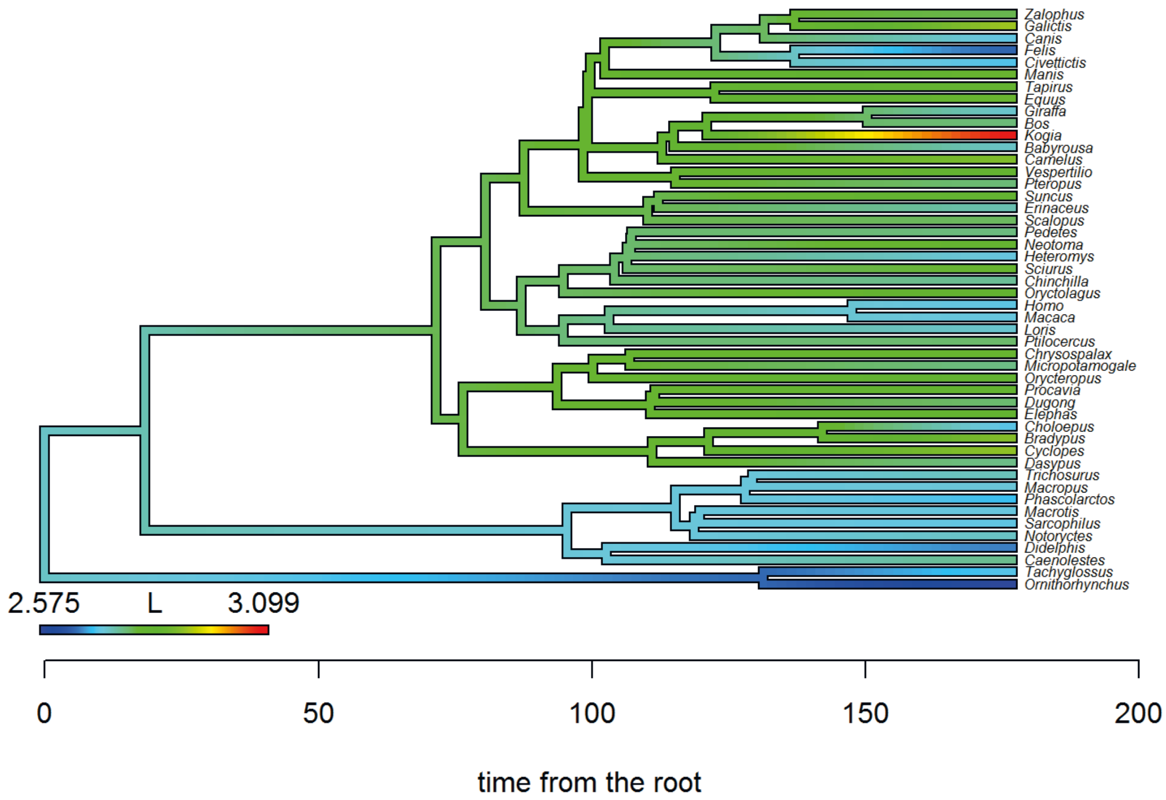

Figure A3 Network average shortest path length (L) mapped on the phylogeny

Table A3 Results of model fitting on trait evolution of network parameters. BM Brownian Motion model; EB Early Burst model; OU Ornbeck-Uhlenstein model.

	log-likelihood	AIC	AICc	ΔAIC	AIC weights
BM	-86.5608	177.1216	177.3883	0	0.541594
EB	-86.2979	178.5957	179.1412	1.4741	0.259165
OU	-86.5608	179.1216	179.6671	2	0.199241

Relative Variability of Network Parameters

Table A4 Results of pair-wise asymptotic test for the equality of coefficients of variation for network parameters. Asymtotic test values and Bonferroni corrected p-values are above and below the diagonal, respectively. P-values < 0.05 are in bold. P-values that were below < 0.05 before correction are underlined.

	N	K	D	C	L	H	P
N		4.109	3.364	1.098	49.358	6.692	31.896
K	<u>0.896</u>		0.039	0.981	70.573	20.115	52.179
D	1.000	1.000		0.632	68.541	18.569	50.154
C	1.000	1.000	1.000		60.267	12.830	42.080
L	**0.000**	**0.000**	**0.000**	**0.000**		24.213	3.067
H	<u>0.203</u>	**0.000**	**0.000**	**0.007**	**0.000**		11.040
P	**0.000**	**0.000**	**0.000**	**0.000**	1.000	**0.019**	

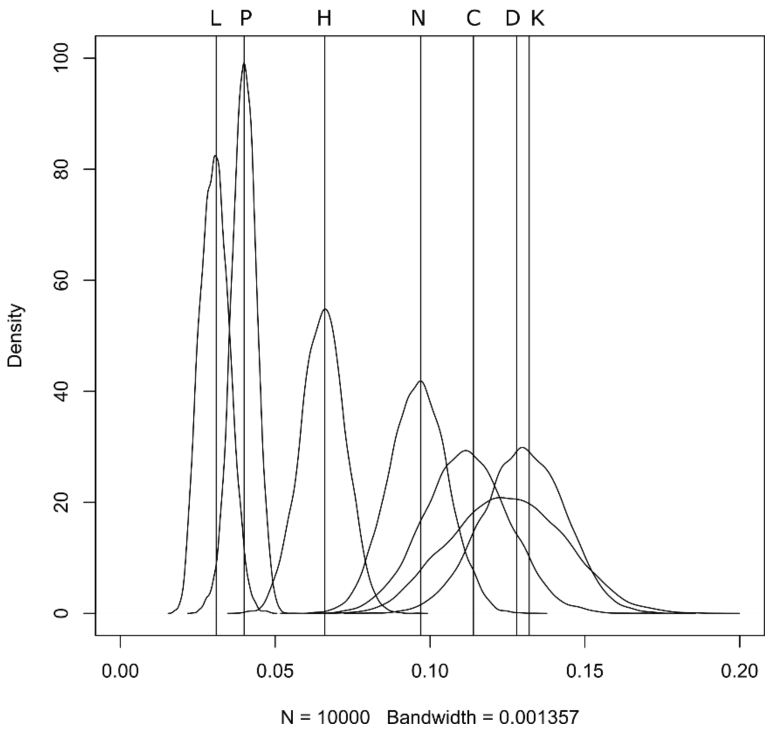

Figure A4 Distribution of coefficients of variation from the network parameters

Community structure and modularity

Table A5 Summary of the modularity analysis

	Modules (M)	Q value	Q expected error	Parcellation (P)
Babyrousa babyrussa	6	0.3157534	0.0279366	0.7842649
Bos taurus	5	0.3570920	0.0289084	0.7690329
Bradypus tridactylus	5	0.4107779	0.0279242	0.7828099
Caenolestes fuliginosus	5	0.3289442	0.0257673	0.7704918
Camelus bactrianus	5	0.4276531	0.0329551	0.7714844
Canis lupus	5	0.3742136	0.0271834	0.7837927
Chinchilla lanigera	7	0.3234277	0.0287324	0.8237311
Choloepus didactylus	6	0.3588158	0.0328270	0.7876543
Chrysospalax trevelyani	4	0.3576601	0.0278696	0.7240115
Civettictis civetta	5	0.3340317	0.0273956	0.7535437
Cyclopes didactylus	7	0.3671672	0.0324112	0.8196615
Dasypus novemcinctus	7	0.3461030	0.0313319	0.8106371
Didelphis virginiana	5	0.3149897	0.0264548	0.7513717
Dugong dugon	6	0.3470239	0.0286939	0.7953008
Elephas maximus	5	0.4066538	0.0298776	0.7760331
Equus caballus	6	0.4095849	0.0277378	0.7855099
Erinaceus europaeus	4	0.3202525	0.0290442	0.7337278
Felis silvestris	5	0.3157275	0.0287367	0.7840513
Galictis cuja	5	0.4156813	0.0280701	0.7795174
Giraffa camelopardalis	5	0.3596841	0.0298892	0.7933428
Heteromys desmarestianus	6	0.3135210	0.0311058	0.7949219
Homo sapiens	5	0.3755961	0.0283249	0.7930143
Kogia breviceps	7	0.4761160	0.0329074	0.8246528
Loris tardigradus	6	0.3302630	0.0281179	0.8077870
Macaca mulatta	7	0.3247553	0.0273871	0.8118785
Macropus rufus	4	0.3515929	0.0265834	0.7252870
Macrotis lagotis	7	0.3000523	0.0258054	0.8120833
Manis pentadactyla	5	0.3460312	0.0299786	0.7905107
Micropotamogale ruwenzorii	5	0.3412755	0.0279693	0.7844650
Neotoma fuscipes	5	0.3575422	0.0275174	0.7406944
Notoryctes typhlops	6	0.3146984	0.0271449	0.8051658
Ornithorhynchus anatinus	5	0.3185768	0.0301478	0.7638889
Orycteropus afer	5	0.4051552	0.0301417	0.7850211
Oryctolagus cuniculus	5	0.3527229	0.0277139	0.7863478
Pedetes capensis	6	0.3380556	0.0284042	0.8018176
Phascolarctos cinereus	5	0.3127772	0.0248347	0.7102606
Procavia capensis	6	0.3436721	0.0283184	0.8145180
Pteropus vampyrus	5	0.3740459	0.0302108	0.7318053
Ptilocercus lowii	4	0.3660936	0.0273621	0.7160665
Sarcophilus harrisii	7	0.3197995	0.0260749	0.7789428
Scalopus aquaticus	4	0.3601520	0.0286475	0.7282236

	Modules (M)	Q value	Q expected error	Parcellation (P)
Sciurus vulgaris	5	0.3776944	0.0258325	0.7591716
Suncus murinus	6	0.3542893	0.0293603	0.7527737
Tachyglossus aculeatus	6	0.3371228	0.0321765	0.7916955
Tapirus indicus	6	0.3817704	0.0290636	0.8054786
Trichosurus vulpecula	4	0.3307777	0.0273543	0.7250231
Vespertilio murinus	4	0.3902735	0.0311857	0.7285156
Zalophus californianus	6	0.4106255	0.0269593	0.7848319

Table A6 Connectivity modules identified for *Babyrousa babyrussa*.

ID	p-value	Elements
1	0.07324	C2, C3, C4, iliocostalis.cervicis.left, iliocostalis.cervicis.right, longus.capitis.left, longus.capitis.right, scalenus.medius.left, scalenus.medius.right, serratus.ventralis.cervicis.right, interspinalis.1, interspinalis.2, interspinalis.3, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.3.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.3.right, intertransversarius.ventralis.longus.left, intertransversarius.ventralis.longus.right
2	0.00017	C5, C6, C7, thoracic.spine, complexus.left, complexus.right, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.left, longissimus.cervicis.right, longus.colli.left, longus.colli.right, rhomboideus.cervicis.left, rhomboideus.cervicis.right, scalenus.ventralis.left, scalenus.ventralis.right, spinalis.cervicis.left, spinalis.cervicis.right, interspinalis.4, interspinalis.5, interspinalis.6, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.4.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.4.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right
3	0.00149	cranium, C1, humerus.left, biventer.cervicis.left, biventer.cervicis.right, cephalohumeralis.left, cleidomastoideus.left, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, splenius.left, splenius.right
4	0.78916	scapula.left, atlantoscapularis.ventralis.left, omohyoideus.left, rhomboideus.capitis.left, serratus.ventralis.cervicis.left, trapezius.left
5	0.40832	scapula.right, humerus.right, atlantoscapularis.ventralis.right, cephalohumeralis.right, cleidomastoideus.right, omohyoideus.right, rhomboideus.capitis.right, trapezius.right
6	0.04049	sternum, hyoid, thyroid, ribs.left, ribs.right, scalenus.dorsalis.left, scalenus.dorsalis.right, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right

Table A7 Connectivity modules identified for *Bos taurus*.

ID	p-value	Elements
1	0.15196	scapula.left, scapula.right, nuchal.ligament, omotransversarius.left, omotransversarius.right, rhomboideus.cervicis.left, rhomboideus.cervicis.right, trapezius.left, trapezius.right
2	4e-05	cranium, C1, humerus.left, humerus.right, cleidomastoideus.left, cleidomastoideus.right, cleidooccipitalis.left, cleidooccipitalis.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, splenius.capitis.left, splenius.capitis.right, splenius.cervicis.left, splenius.cervicis.right
3	7e-05	C5, C6, C7, thoracic.spine, iliocostalis.cervicis.left, iliocostalis.cervicis.right, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.left, longissimus.cervicis.right, longus.colli.right, scalenus.medius.left, scalenus.medius.right, scalenus.ventralis.left, scalenus.ventralis.right, semispinalis.capitis.left, semispinalis.capitis.right, semispinalis.cervicis.left, semispinalis.cervicis.right, interspinalis.4, interspinalis.5, interspinalis.6, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.4.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.4.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right
4	0.00266	mandible, sternum, hyoid, thyroid, ribs.left, ribs.right, scalenus.dorsalis.left, scalenus.dorsalis.right, sternohyoideus.left, sternohyoideus.right, sternomandibularis.left, sternomandibularis.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right
5	0.04034	C2, C3, C4, longus.capitis.left, longus.capitis.right, longus.colli.left, omohyoideus.left, omohyoideus.right, serratus.ventralis.cervicis.left, serratus.ventralis.cervicis.right, interspinalis.1, interspinalis.2, interspinalis.3, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.3.left, intertransversarius.ventralis.longus.left, intertransversarius.ventralis.longus.right, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.3.right

Table A8 Connectivity modules identified for *Bradypus tridactylus*.

ID	p-value	Elements
1	0.00044	C2, C3, C4, C5, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.left, longissimus.cervicis.right, scalenus.anticus.left, scalenus.anticus.right, semispinalis.capitis.left, semispinalis.capitis.right, semispinalis.cervicis.left, semispinalis.cervicis.right, splenius.capitis.left, splenius.capitis.right, splenius.cervicis.left, splenius.cervicis.right, interspinalis.1, interspinalis.2, interspinalis.3, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.3.left, intertransversarius.ventralis.1.left, intertransversarius.ventralis.2.left, intertransversarius.ventralis.3.left, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.3.right, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right, intertransversarius.ventralis.3.right
2	0.00103	cranium, C1, cleido.mastoideus.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right
3	0.00125	clavicle.left, clavicle.right, sternum, hyoid, thyroid, ribs.left, ribs.right, clavotrapezius.left, clavotrapezius.right, cleido.mastoideus.left, sternocleidomastoideus.left, sternocleidomastoideus.right, sternohyoid.left, sternohyoid.right, sternothyroideus.left, sternothyroideus.right
4	0.01892	C6, C7, iliocostalis.cervicis.left, iliocostalis.cervicis.right, longus.capitis.left, longus.capitis.right, scalenus.posticus.left, scalenus.posticus.right, interspinalis.4, interspinalis.5, interspinalis.6, intertransversarius.dorsalis.4.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.4.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, intertransversarius.dorsalis.4.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.4.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right
5	0.00244	C8, C9, thoracic.spine, scapula.left, scapula.right, longus.colli.left, longus.colli.right, rhomboideus.cervicis.left, rhomboideus.cervicis.right, serratus.ventralis.cervicis.left, serratus.ventralis.cervicis.right, trapezius.left, trapezius.right, interspinalis.7, interspinalis.8, intertransversarius.dorsalis.7.left, intertransversarius.dorsalis.8.left, intertransversarius.ventralis.7.left, intertransversarius.ventralis.8.left, intertransversarius.dorsalis.7.right, intertransversarius.dorsalis.8.right, intertransversarius.ventralis.7.right, intertransversarius.ventralis.8.right

Table A9 Connectivity modules identified for *Caenolestes fuliginosus*.

ID	p-value	Elements
1	0.02453	sternum, hyoid, thyroid, ribs.right, longus.colli.right, omohyoideus.left, omohyoideus.right, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right
2	0.53254	C2, complexus.left, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.superficialis.left, rectus.capitis.dorsalis.superficialis.right, interspinalis.1, intertransversarii.dorsalis.1.left, intertransversarii.ventralis.1.left, intertransversarii.dorsalis.1.right, intertransversarii.ventralis.1.right
3	0.04481	C6, C7, thoracic.spine, ribs.left, iliocostalis.dorsi.left, iliocostalis.dorsi.right, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.left, longissimus.cervicis.right, longus.colli.left, semispinalis.cervicis.left, semispinalis.cervicis.right, splenius.left, splenius.right, interspinalis.5, interspinalis.6, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarii.dorsalis.4.left, intertransversarii.dorsalis.5.left, intertransversarii.dorsalis.6.left, intertransversarii.ventralis.5.left, intertransversarii.ventralis.6.left, spinalis.cervicis.left, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarii.dorsalis.5.right, intertransversarii.dorsalis.6.right, intertransversarii.ventralis.4.right, intertransversarii.ventralis.5.right, intertransversarii.ventralis.6.right, spinalis.cervicis.right
4	1e-04	cranium, C1, clavicle.left, clavicle.right, scapula.left, scapula.right, acromiotrapezius.left, atlantoacromialis.left, atlantoacromialis.right, atlantoscapularis.left, atlantoscapularis.right, biventer.cervicis.left, biventer.cervicis.right, cleidomastoideus.left, cleidomastoideus.right, cleidooccipitalis.left, cleidooccipitalis.right, complexus.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, rhomboideus.capitis.left, rhomboideus.capitis.right, rhomboideus.major.left, rhomboideus.major.right
5	0.00011	C3, C4, C5, acromiotrapezius.right, levator.scapulae.left, levator.scapulae.right, longus.capitis.left, longus.capitis.right, scalenus.anticus.left, scalenus.anticus.right, scalenus.medius.left, scalenus.medius.right, interspinalis.2, interspinalis.3, interspinalis.4, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, multifidius.submultifidius.4.left, intertransversarii.dorsalis.2.left, intertransversarii.dorsalis.3.left, intertransversarii.ventralis.2.left, intertransversarii.ventralis.3.left, intertransversarii.ventralis.4.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, multifidius.submultifidius.4.right, intertransversarii.dorsalis.2.right, intertransversarii.dorsalis.3.right, intertransversarii.dorsalis.4.right, intertransversarii.ventralis.2.right, intertransversarii.ventralis.3.right

Table A10 Connectivity modules identified for *Camelus bactrianus*.

ID	p-value	Elements
1	4e-05	C5, C6, C7, thoracic.spine, ribs.left, ribs.right, intertransversarius.dorsalis.4.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, levator.scapulae.left, longissimus.cervicis.left, longus.colli.left, multifius.4.left, scalenus.primocostal.left, scalenus.supracostal.left, spinalis.cervicis.left, intertransversarius.dorsalis.4.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, levator.scapulae.right, longissimus.cervicis.right, longus.colli.right, multifius.4.right, scalenus.primocostal.right, scalenus.supracostal.right, spinalis.cervicis.right
2	0.00168	scapula.left, scapula.right, humerus.left, humerus.right, nuchal.ligament, mastohumeralis.left, omotransversalis.left, rhomboideus.cervicis.left, mastohumeralis.right, omotransversalis.right, rhomboideus.cervicis.right
3	0.00395	C2, C3, C4, complexus.minor.left, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.3.left, intertransversarius.ventralis.brevis.1.left, intertransversarius.ventralis.brevis.2.left, intertransversarius.ventralis.brevis.3.left, intertransversarius.ventralis.longus.left, longus.capitis.left, multifius.1.left, multifius.2.left, multifius.3.left, omohyoideus.left, complexus.minor.right, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.3.right, intertransversarius.ventralis.brevis.1.right, intertransversarius.ventralis.brevis.2.right, intertransversarius.ventralis.brevis.3.right, intertransversarius.ventralis.longus.right, longus.capitis.right, multifius.1.right, multifius.2.right, multifius.3.right, omohyoideus.right
4	0.00075	mandible, sternum, hyoid, thyroid, sternohyoideus.left, sternomatoideus.left, sternomaxillaris.left, sternothyroideus.left, sternohyoideus.right, sternomatoideus.right, sternomaxillaris.right, sternothyroideus.right
5	0.00023	cranium, C1, complexus.major.left, longus.atlantis.left, obliquus.capitis.caudalis.left, obliquus.capitis.cranialis.left, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.minor.left, rectus.capitis.lateralis.left, rectus.capitis.ventralis.left, complexus.major.right, longus.atlantis.right, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.right, rectus.capitis.ventralis.right

Table A11 Connectivity modules identified for *Canis lupus*.

ID	p-value	Elements
1	0.00152	sternum, hyoid, thyroid, ribs.left, ribs.right, scalenus.supracostalis.left, scalenus.supracostalis.right, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternooccipitalis.left, sternooccipitalis.right, sternothyroideus.left, sternothyroideus.right
2	0.00211	C2, C3, C4, longus.capitis.left, longus.capitis.right, longus.colli.left, longus.colli.right, semispinalis.cervicis.left, semispinalis.cervicis.right, spinalis.cervicis.left, spinalis.cervicis.right, interspinalis.1, interspinalis.2, interspinalis.3, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarii.dorsalis.1.left, intertransversarii.dorsalis.2.left, intertransversarii.dorsalis.3.left, intertransversarii.ventralis.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarii.dorsalis.1.right, intertransversarii.dorsalis.2.right, intertransversarii.dorsalis.3.right, intertransversarii.ventralis.right, intertransversarius.intermedius.1.right, intertransversarius.intermedius.2.right, intertransversarius.intermedius.3.right, intertransversarius.intermedius.1.left, intertransversarius.intermedius.2.left, intertransversarius.intermedius.3.left
3	1e-04	cranium, C1, scapula.left, humerus.left, biventer.cervicis.left, cleidocervicalis.left, cleidomastoideus.left, levator.claviculae.left, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.intermedius.left, rectus.capitis.dorsalis.intermedius.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, rhomboideus.capitis.left
4	0.0024	ligamentum.nuchae, scapula.right, thoracic.spine, humerus.right, biventer.cervicis.right, cleidocervicalis.right, cleidomastoideus.right, levator.claviculae.right, rhomboideus.capitis.right, rhomboideus.cervicis.left, rhomboideus.cervicis.right, splenius.left, splenius.right, trapezius.left, trapezius.right, interspinalis.6, intertransversarii.dorsalis.5.left, intertransversarii.dorsalis.6.left, intertransversarii.dorsalis.5.right, intertransversarii.dorsalis.6.right
5	0.00523	C5, C6, C7, complexus.left, complexus.right, longissimus.atlantis.left, longissimus.atlantis.right, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.left, longissimus.cervicis.right, scalenus.primae.costae.left, scalenus.primae.costae.right, serratus.ventralis.cervicis.left, serratus.ventralis.cervicis.right, interspinalis.4, interspinalis.5, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarii.dorsalis.4.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarii.dorsalis.4.right, intertransversarius.intermedius.4.right, intertransversarius.intermedius.5.right, intertransversarius.intermedius.6.right, intertransversarius.intermedius.4.left, intertransversarius.intermedius.5.left, intertransversarius.intermedius.6.left

Table A12 Connectivity modules identified for *Chinchilla lanigera*.

ID	p-value	Elements
1	0.91792	ribs.right, scalenus.anticus.right, scalenus.medius.right
2	0.12543	C2, C3, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, scalenus.medius.left, serratus.ventralis.left, splenius.left, splenius.right, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.ventralis.1.left, intertransversarius.ventralis.2.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right
3	0.9094	scapula.right, levator.claviculae.right, levator.scapulae.right, rhomboideus.capitis.right, rhomboideus.right, trapezius.right
4	0.0014	cranium, C1, scapula.left, biventer.cervicis.left, biventer.cervicis.right, levator.claviculae.left, levator.scapulae.left, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, rhomboideus.capitis.left, rhomboideus.left, trapezius.left
5	0.00026	clavicle.left, clavicle.right, sternum, hyoid, thyroid, ribs.left, cleidomastoideus.left, cleidomastoideus.right, scalenus.anticus.left, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right
6	0.02974	C4, C5, C6, complexus.left, iliocostalis.cervicis.left, iliocostalis.cervicis.right, longissimus.cervicis.left, longissimus.cervicis.right, longus.capitis.left, longus.capitis.right, serratus.ventralis.right, spinalis.cervicis.left, spinalis.cervicis.right, splenius.capitis.left, splenius.capitis.right, multifidius.submultifidius.3.left, intertransversarius.dorsalis.3.left, intertransversarius.dorsalis.4.left, intertransversarius.ventralis.3.left, intertransversarius.ventralis.4.left, multifidius.submultifidius.3.right, intertransversarius.dorsalis.3.right, intertransversarius.dorsalis.4.right, intertransversarius.ventralis.3.right, intertransversarius.ventralis.4.right
7	0.03537	C7, thoracic.spine, complexus.right, longus.colli.left, longus.colli.right, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right

Table A13 Connectivity modules identified for *Choloepus didactylus*.

ID	p-value	Elements
1	0.41149	clavicle.right, scapula.right, cleido.mastoideus.right, levator.claviculae.right, rhomboideus.capitis.right, serratus.ventralis.cervicis.right, trapezius.right
2	0.00125	cranium, C1, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right
3	0.41149	clavicle.left, scapula.left, cleido.mastoideus.left, levator.claviculae.left, rhomboideus.capitis.left, serratus.ventralis.cervicis.left, trapezius.left
4	0.00211	C5, C6, thoracic.spine, iliocostalis.cervicis.left, iliocostalis.cervicis.right, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.left, longissimus.cervicis.right, longus.capitis.left, longus.capitis.right, rhomboideus.cervicis.left, rhomboideus.cervicis.right, semispinalis.capitis.left, interspinalis.4, interspinalis.5, intertransversarius.dorsalis.4.left, intertransversarius.dorsalis.5.left, intertransversarius.ventralis.4.left, intertransversarius.ventralis.5.left, intertransversarius.dorsalis.4.right, intertransversarius.dorsalis.5.right, intertransversarius.ventralis.4.right, intertransversarius.ventralis.5.right
5	0.07576	C2, C3, C4, longus.colli.left, longus.colli.right, scalenus.posticus.left, scalenus.posticus.right, semispinalis.capitis.right, splenius.capitis.left, splenius.capitis.right, splenius.cervicis.left, splenius.cervicis.right, interspinalis.1, interspinalis.2, interspinalis.3, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.3.left, intertransversarius.ventralis.1.left, intertransversarius.ventralis.2.left, intertransversarius.ventralis.3.left, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.3.right, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right, intertransversarius.ventralis.3.right
6	0.00625	sternum, hyoid, thyroid, ribs.left, ribs.right, sternohyoid.left, sternohyoid.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right

Table A14 Connectivity modules identified for *Chrysospalax trevelyani*.

ID	p-value	Elements
1	0.01538	sternum, hyoid, thyroid, ribs.left, iliocostalis.cervicis.left, omohyoid.left, omohyoid.right, sternohyoid.left, sternohyoid.right, sternomastoideus.left, sternomastoideus.right, sternothyroid.left, sternothyroid.right
2	0	cranium, C1, scapula.left, scapula.right, clavicula.left, clavicula.right, biventer.cervicis.left, biventer.cervicis.right, cleidomastoid.left, cleidomastoid.right, cleidooccipitalis.left, cleidooccipitalis.right, levator.claviculae.left, levator.claviculae.right, levator.scapulae.left, levator.scapulae.right, longus.capitis.left, longus.capitis.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.lateralis.right.1, rectus.capitis.ventralis.left, rhomboideus.capitis.left, rhomboideus.capitis.right
3	0.00036	C2, C3, C4, C5, complexus.left, complexus.right, longissimus.cervicis.left, longissimus.cervicis.right, scalenus.ventralis.left, scalenus.ventralis.right, serratus.ventralis.cervicis.left, serratus.ventralis.cervicis.right, trapezius.left, trapezius.right, interspinalis.1, interspinalis.2, interspinalis.3, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, multifidius.submultifidius.4.left, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.3.left, intertransversarius.ventralis.1.left, intertransversarius.ventralis.2.left, intertransversarius.ventralis.3.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, multifidius.submultifidius.4.right, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.3.right, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right, intertransversarius.ventralis.3.right
4	0.00338	C6, C7, thoracic.spine, ribs.right, iliocostalis.cervicis.right, longissimus.capitis.left, longissimus.capitis.right, rhomboideus.cervicis.left, rhomboideus.cervicis.right, splenius.left, splenius.right, interspinalis.4, interspinalis.5, interspinalis.6, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.4.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.4.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.4.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.4.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right

Table A15 Connectivity modules identified for *Civettictis civetta*.

ID	p-value	Elements
1	0.00017	C5, C6, C7, thoracic.spine, complexus.left, complexus.right, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.left, longissimus.cervicis.right, longus.colli.right, rhomboideus.cervicis.left, semispinalis.cervicis.left, semispinalis.cervicis.right, serratus.ventralis.cervicis.left, spinalis.cervicis.left, spinalis.cervicis.right, splenius.cervicis.left, splenius.cervicis.rigth, trapezius.left, interspinalis.4, interspinalis.5, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, intertransversarii.dorsalis.5.left, intertransversarii.dorsalis.6.left, intertransversarii.dorsalis.7.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, intertransversarii.dorsalis.5.right, intertransversarii.dorsalis.6.right, intertransversarii.dorsalis.7.right, intertransversarius.intermedius.4.right, intertransversarius.intermedius.4.left
2	0.95091	scapula.right, levator.claviculae.right, rhomboideus.cervicis.right, serratus.ventralis.cervicis.right, trapezius.right
3	0.00051	C2, C3, C4, longus.capitis.left, longus.capitis.right, longus.colli.left, interspinalis.1, interspinalis.2, interspinalis.3, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarii.dorsalis.2.left, intertransversarii.dorsalis.3.left, intertransversarii.dorsalis.4.left, intertransversarii.ventralis.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarii.dorsalis.2.right, intertransversarii.dorsalis.3.right, intertransversarii.dorsalis.4.right, intertransversarii.ventralis.right, intertransversarius.intermedius.1.right, intertransversarius.intermedius.2.right, intertransversarius.intermedius.3.right, intertransversarius.intermedius.1.left, intertransversarius.intermedius.2.left, intertransversarius.intermedius.3.left
4	0.00086	sternum, hyoid, thyroid, ribs.left, ribs.right, scalenus.primae.costae.left, scalenus.primae.costae.right, scalenus.supracostalis.left, scalenus.supracostalis.right, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right
5	4e-05	cranium, C1, scapula.left, humerus.left, humerus.right, biventer.cervicis.left, biventer.cervicis.right, cleidocervicalis.left, cleidocervicalis.right, cleidomastoideus.left, cleidomastoideus.right, levator.claviculae.left, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.intermedius.left, rectus.capitis.dorsalis.intermedius.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, splenius.capitis.left, splenius.capitis.right, intertransversarii.dorsalis.1.left, intertransversarii.dorsalis.1.right

Table A16 Connectivity modules identified for *Cyclopes didactylus*.

ID	p-value	Elements
1	0.00077	cranium, C1, longissimus.capitis.left, longissimus.capitis.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right
2	0.07221	C2, C3, C4, thoracic.spine, longissimus.cervicis.left, longissimus.cervicis.right, longus.capitis.right, longus.colli.left, longus.colli.right, rhomboideus.cervicis.left, rhomboideus.cervicis.right, semispinalis.capitis.left, semispinalis.capitis.right, splenius.capitis.left, splenius.capitis.right, interspinalis.1, interspinalis.2, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.ventralis.1.left, intertransversarius.ventralis.2.left, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right
3	0.55235	C5, interspinalis.3, interspinalis.4, intertransversarius.dorsalis.3.left, intertransversarius.dorsalis.4.left, intertransversarius.ventralis.3.left, intertransversarius.ventralis.4.left, intertransversarius.dorsalis.3.right, intertransversarius.dorsalis.4.right, intertransversarius.ventralis.3.right, intertransversarius.ventralis.4.right
4	0.36822	clavicle.right, scapula.right, atlantoscapularis.reifht, cleido.mastoideus.right, trapezius.right
5	0.00021	mandible, sternum, hyoid, thyroid, tongue, sterno.mastoideus.left, sterno.mastoideus.right, sterno.maxillaris.left, sterno.maxillaris.right, sternoglossus.left, sternoglossus.right, sternothyroideus.left, sternothyroideus.right
6	0.36822	clavicle.left, scapula.left, atlantoscapularis.left, cleido.mastoideus.left, trapezius.left
7	0.00435	C6, C7, ribs.left, ribs.right, iliocostalis.cervicis.left, iliocostalis.cervicis.right, longus.capitis.left, scalenus.longus.left, scalenus.longus.right, serratus.ventralis.cervicis.left, serratus.ventralis.cervicis.right, interspinalis.5, interspinalis.6, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right

Table A17 Connectivity modules identified for *Dasypus novemcinctus*.

ID	p-value	Elements
1	0.00585	C6, C7, ribs.left, ribs.right, iliocostalis.cervicis.left, iliocostalis.cervicis.right, scalenus.brevis.left, scalenus.brevis.right, scalenus.longus.left, scalenus.longus.right, serratus.ventralis.cervicis.left, serratus.ventralis.cervicis.right, interspinalis.4, interspinalis.5, intertransversarius.dorsalis.4.left, intertransversarius.dorsalis.5.left, intertransversarius.ventralis.4.left, intertransversarius.ventralis.5.left, intertransversarius.dorsalis.4.right, intertransversarius.dorsalis.5.right, intertransversarius.ventralis.4.right, intertransversarius.ventralis.5.right
2	0.22839	clavicle.left, scapula.left, cleido.mastoideus.left, trapezius.left
3	0.75162	thoracic.spine, longissimus.capitis.left, longissimus.capitis.right, semispinalis.capitis.right, interspinalis.6, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.6.left, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.6.right
4	0.22839	clavicle.right, scapula.right, cleido.mastoideus.right, trapezius.right
5	0.00037	mandible, sternum, hyoid, thyroid, sternohyoideus.left, sternohyoideus.right, sterno.mastoideus.left, sterno.mastoideus.right, sterno.maxillaris.left, sterno.maxillaris.right, sternothyroideus.left, sternothyroideus.right
6	0.40099	C3, C4, C5, longissimus.cervicis.left, longissimus.cervicis.right, longus.capitis.left, longus.capitis.right, longus.colli.left, longus.colli.right, semispinalis.capitis.left, splenius.capitis.left, splenius.capitis.right, interspinalis.2, interspinalis.3, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.3.left, intertransversarius.ventralis.2.left, intertransversarius.ventralis.3.left, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.3.right, intertransversarius.ventralis.2.right, intertransversarius.ventralis.3.right
7	0.00045	cranium, C1, C2, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, rhomboideus.cervicis.left, rhomboideus.cervicis.right, interspinalis.1, intertransversarius.dorsalis.1.left, intertransversarius.ventralis.1.left, intertransversarius.dorsalis.1.right, intertransversarius.ventralis.1.right

Table A18 Connectivity modules identified for *Didelphis virginiana*.

ID	p-value	Elements
1	5e-05	C6, C7, thoracic.spine, ribs.left, ribs.right, cervicalis.ascendens.left, cervicalis.ascendens.right, complexus.left, iliocostalis.dorsi.left, iliocostalis.dorsi.right, multifidius.submultifidius.1.left, multifidius.submultifidius.1.right, scalenus.anticus.left, scalenus.anticus.right, scalenus.posticus.left, scalenus.posticus.right, semispinalis.cervicis.left, semispinalis.cervicis.right, splenius.right, interspinalis.1, interspinalis.2, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarii.ventralis.4.left, intertransversarii.ventralis.5.left, intertransversarii.ventralis.6.left, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarii.ventralis.4.right, intertransversarii.ventralis.5.right, intertransversarii.ventralis.6.right
2	0.00245	sternum, hyoid, thyroid, omohyoid.left, omohyoid.right, sternohyoideus.left, sternohyoideus.right, sternothyroid.left, sternothyroid.right, sternomastoideus.left, sternomastoideus.right
3	0.00032	C2, C3, C4, C5, intertransversarii.dorsalis.longi.left, intertransversarii.dorsalis.longi.right, levator.scapulae.right, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.left, longissimus.cervicis.right, longus.capitis.left, longus.colli.left, longus.colli.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, spinalis.cervicis.left, spinalis.cervicis.right, splenius.left, multifidius.submultifidius.1.left.1, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, multifidius.submultifidius.4.left, intertransversarii.ventralis.1.left, intertransversarii.ventralis.2.left, intertransversarii.ventralis.3.left, multifidius.submultifidius.1.right.1, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, multifidius.submultifidius.4.right, intertransversarii.ventralis.1.right, intertransversarii.ventralis.2.right, intertransversarii.ventralis.3.right
4	0.00392	cranium, C1, clavicle.right, scapula.right, atlantoacromialis.right, atlantoscapularis.right, biventer.cervicis.left, biventer.cervicis.right, cleidomastoideus.right, complexus.right, longus.capitis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.dorsalis.superficialis.left, rectus.capitis.dorsalis.superficialis.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, rhomboideus.right, trapezius.right
5	0.68552	clavicle.left, scapula.left, atlantoacromialis.left, atlantoscapularis.left, cleidomastoideus.left, levator.scapulae.left, rhomboideus.left, trapezius.left

Table A19 Connectivity modules identified for *Dugong dugon*.

ID	p-value	Elements
1	0.02227	cranium, C1, scapula.left, humerus.left, brachiocephalicus.left, cephalohumeralis.left, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.intermedius.left, rectus.capitis.intermedius.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, semispinalis.capitis.left, semispinalis.capitis.right, spinalis.cervicis, spinalis.cervicis.1
2	0.0187	sternum, hyoid, thyroid, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right
3	0.00838	C5, C6, longissimus.capitis.right, longus.capitis.left, longus.capitis.right, semispinalis.dorsi.left, interspinalis.3, interspinalis.4, multifidius.submultifidius.3.left, multifidius.submultifidius.4.left, intertransversarius.dorsalis.3.left, intertransversarius.dorsalis.4.left, intertransversarius.dorsalis.5.left, intertransversarius.ventralis.3.left, intertransversarius.ventralis.4.left, multifidius.submultifidius.3.right, multifidius.submultifidius.4.right, intertransversarius.dorsalis.3.right, intertransversarius.dorsalis.4.right, intertransversarius.dorsalis.5.right, intertransversarius.ventralis.3.right, intertransversarius.ventralis.4.right, intertransversarius.ventralis.5.right
4	0.45549	scapula.right, humerus.right, brachiocephalicus.right, cephalohumeralis.right, trapezius.right
5	0.00297	C2, C3, C4, longissimus.dorsi.left, longissimus.dorsi.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, scalenus.anterior.left, scalenus.anterior.right, semispinalis.dorsi.right, serratus.magnus.left, serratus.magnus.right, trapezius.left, interspinalis.1, interspinalis.2, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.ventralis.1.left, intertransversarius.ventralis.2.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right
6	0.00531	C7, thoracic.spine, ribs.left, ribs.right, iliocostalis.cervicis.left, iliocostalis.cervicis.right, longissimus.capitis.left, longus.colli.left, longus.colli.right, rhomboideus.cervicis.left, rhomboideus.cervicis.right, interspinalis.5, interspinalis.6, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.6.right

Table A20 Connectivity modules identified for *Elephas maximus*.

ID	p-value	Elements
1	0.5	C2, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.externus.left, rectus.capitis.externus.right, interspinalis.1, multifidius.submultifidius.1.left, intertransversarius.dorsalis.1.left, intertransversarius.ventralis.1.left, multifidius.submultifidius.1.right, intertransversarius.dorsalis.1.right, intertransversarius.ventralis.1.right
2	0.00285	mandible, sternum, hyoid, thyroid, ribs.left, ribs.right, sternomandibularis.left, sternomandibularis.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right
3	0.00035	C3, C4, C5, levator.scapulae.left, levator.scapulae.right, longus.capitis.left, longus.capitis.right, longus.colli.left, longus.colli.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, scalenus.anterior.left, scalenus.anterior.right, interspinalis.2, interspinalis.3, multifidius.submultifidius.2.left, multifidius.submultifidius.4.left, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.3.left, intertransversarius.ventralis.2.left, intertransversarius.ventralis.3.left, intertransversarius.ventralis.4.left, multifidius.submultifidius.2.right, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.3.right, intertransversarius.dorsalis.4.right, intertransversarius.ventralis.2.right, intertransversarius.ventralis.3.right
4	0	cranium, C1, scapula.left, scapula.right, humerus.left, humerus.right, nuchal.ligament, levator.anguli.scapulae.left, levator.anguliscapulae.right, mastohumeralis.left, mastohumeralis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, occipitoscapularis.left, occipitoscapularis.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rhomboideus.cervicis.left, rhomboideus.cervicis.right, splenius.left, splenius.right, trapezius.left, trapezius.right
5	0.00167	C6, C7, thoracic.spine, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.left, longissimus.cervicis.right, semispinalis.capitis.left, semispinalis.capitis.right, semispinalis.cervicis.left, semispinalis.cervicis.right, interspinalis.4, interspinalis.5, interspinalis.6, multifidius.submultifidius.3.left, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.4.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, multifidius.submultifidius.3.right, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.4.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right

Table A21 Connectivity modules identified for *Equus caballus*.

ID	p-value	Elements
1	0.00055	mandible, sternum, hyoid, thyroid, omohyoideus.left, sternohyoideus.left, sternohyoideus.right, sternomandibularis.left, sternomandibularis.right, sternothyroideus.left, sternothyroideus.right
2	0	C5, C6, C7, ribs.left, ribs.right, iliocostalis.cervicis.left, iliocostalis.cervicis.right, longissimus.cervicis.left, longissimus.cervicis.right, scalenus.medius.left, scalenus.medius.right, scalenus.ventralis.left, scalenus.ventralis.right, serratus.ventralis.cervicis.left, spinalis.cervicis.left, spinalis.cervicis.right, interspinalis.4, interspinalis.5, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.4.left, intertransversarius.dorsalis.5.left, intertransversarius.ventralis.4.left, intertransversarius.ventralis.5.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.4.right, intertransversarius.dorsalis.5.right, intertransversarius.ventralis.4.right, intertransversarius.ventralis.5.right, intertransversarius.intermedius.5.left, intertransversarius.intermedius.5.right
3	0.42899	scapula.right, humerus.right, cleidomastoideus.right, omohyoideus.right, omotransversarius.right, serratus.ventralis.cervicis.right
4	0.00023	cranium, C1, scapula.left, humerus.left, cleidomastoideus.left, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, omotransversarius.left, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, semispinalis.capitis.b.left, semispinalis.capitis.b.right
5	0.04537	thoracic.spine, nuchal.ligament, longissimus.atlantis.left, longissimus.atlantis.right, longissimus.capitis.left, longissimus.capitis.right, rhomboideus.cervicis.left, rhomboideus.cervicis.right, splenius.capitis.left, splenius.capitis.right, trapezius.left, trapezius.right, interspinalis.6, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.6.left, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.6.right
6	4e-05	C2, C3, C4, longus.capitis.left, longus.capitis.right, longus.colli.left, longus.colli.right, splenius.cervicis.left, splenius.cervicis.right, interspinalis.1, interspinalis.2, interspinalis.3, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.3.left, intertransversarius.ventralis.1.left, intertransversarius.ventralis.2.left, intertransversarius.ventralis.3.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.3.right, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right, intertransversarius.ventralis.3.right, intertransversarius.intermedius.2.left, intertransversarius.intermedius.3.left, intertransversarius.intermedius.4.left, intertransversarius.intermedius.2.right, intertransversarius.intermedius.3.right, intertransversarius.intermedius.4.right

Table A22 Connectivity modules identified for *Erinaceus europaeus*.

ID	p-value	Elements
1	0.00071	cranium, C1, clavicle.left, scapula.left, cleido.mastoideus.left, cleido.occipitalis.left, levator.scapulae.left, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, rhomboideus.cervicis.left
2	0.00139	clavicle.right, scapula.right, sternum, hyoid, thyroid, ribs.left, ribs.right, cleido.mastoideus.right, cleido.occipitalis.right, iliocostalis.cervicis.left, iliocostalis.cervicis.right, levator.scapulae.right, omohyoideus.left, omohyoideus.right, sternohyoideus.left, sternohyoideus.right, sterno.mastoideus.left, sterno.mastoideus.right, sternothyroideus.left, sternothyroideus.right
3	0.00077	C5, C6, C7, thoracic.spine, longissimus.capitis.left, longissimus.capitis.right, longus.atlantis.left, longus.atlantis.right, longus.capitis.left, longus.capitis.right, longus.colli.right, rhomboideus.cervicis.right, semispinalis.capitis.left, semispinalis.capitis.right, semispinalis.cervicis.left, semispinalis.cervicis.right, splenius.left, splenius.right, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.4.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.4.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.4.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.4.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right
4	0.01809	C2, C3, C4, longus.colli.left, scalenus.left, scalenus.right, serratus.ventralis.cervicis.left, serratus.ventralis.cervicis.right, trapezius.anticus.left, trapezius.anticus.right, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.3.left, intertransversarius.ventralis.1.left, intertransversarius.ventralis.2.left, intertransversarius.ventralis.3.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.3.right, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right, intertransversarius.ventralis.3.right

Table A23 Connectivity modules identified for *Felis silvestris*.

ID	p-value	Elements
1	0.05328	C2, C3, acromiotrapezius.left, longus.atlantis.left, longus.atlantis.right, longus.colli.right, rectus.capitis.dorsalis.intermedius.left, rectus.capitis.dorsalis.major.right, scalenus..right, interspinalis.1, interspinalis.2, intertransversarii.dorsalis.1.left, intertransversarii.dorsalis.2.left, intertransversarii.dorsalis.3.left, intertransversarii.dorsalis.2.right, intertransversarii.dorsalis.3.right, intertransversarius.intermedius.1.right, intertransversarius.intermedius.2.right, intertransversarius.intermedius.1.left, intertransversarius.intermedius.2.left
2	0	cranium, C1, scapula.left, scapula.right, humerus.left, humerus.right, cleidocervicalis.left, cleidocervicalis.right, cleidomastoideus.left, cleidomastoideus.right, levator.claviculae.left, levator.claviculae.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.intermedius.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, rhomboideus.capitis.left, rhomboideus.capitis.right, intertransversarii.dorsalis.1.right
3	0.14192	C4, C5, C6, complexus.left, complexus.right, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.left, longissimus.cervicis.right, longus.capitis.left, longus.capitis.right, serratus.ventralis.cervicis.left, serratus.ventralis.cervicis.right, spinalis.cervicis.left, spinalis.cervicis.right, interspinalis.3, interspinalis.4, intertransversarii.dorsalis.4.left, intertransversarii.dorsalis.5.left, intertransversarii.ventralis.left, intertransversarii.dorsalis.4.right, intertransversarii.dorsalis.5.right, intertransversarii.ventralis.right, intertransversarius.intermedius.3.right, intertransversarius.intermedius.4.right, intertransversarius.intermedius.3.left, intertransversarius.intermedius.4.left
4	0.00203	sternum, hyoid, thyroid, ribs.left, ribs.right, scalenus.left, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right
5	0.69676	C7, thoracic.spine, acromiotrapezius.right, biventer.cervicis.left, biventer.cervicis.right, longus.colli.left, rhomboideus.cervicis.left, rhomboideus.cervicis.right, semispinalis.cervicis.left, semispinalis.cervicis.right, splenius.cervicis.left, splenius.cervicis.rigth, interspinalis.5, intertransversarii.dorsalis.6.left, intertransversarii.dorsalis.7.left, intertransversarii.dorsalis.6.right, intertransversarii.dorsalis.7.right

Table A24 Connectivity modules identified for *Galictis cuja*.

ID	p-value	Elements
1	0.00196	C2, C3, C4, interspinalis.1, interspinalis.2, intertransversarii.dorsalis.2.left, intertransversarii.dorsalis.2.right, intertransversarii.dorsalis.3.left, intertransversarii.dorsalis.3.right, intertransversarii.dorsalis.4.left, intertransversarii.ventralis.left, intertransversarii.ventralis.right, intertransversarius.intermedius.1.left, intertransversarius.intermedius.1.right, intertransversarius.intermedius.2.left, intertransversarius.intermedius.2.right, intertransversarius.intermedius.3.left, longissimus.cervicis.right, longus.capitis.left, longus.capitis.right, longus.colli.left, multifidius.submultifidius.1.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.left, multifidius.submultifidius.2.right, multifidius.submultifidius.3.left, multifidius.submultifidius.3.right, spinalis.cervicis.right
2	0.00472	C5, C6, C7, ribs.left, complexus.left, complexus.right, interspinalis.3, interspinalis.4, interspinalis.5, intertransversarii.dorsalis.4.right, intertransversarii.dorsalis.5.left, intertransversarii.dorsalis.5.right, intertransversarii.dorsalis.6.left, intertransversarii.dorsalis.6.right, intertransversarius.intermedius.3.right, intertransversarius.intermedius.4.left, intertransversarius.intermedius.4.right, longissimus.cervicis.left, longus.colli.right, multifidius.submultifidius.4.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.left, multifidius.submultifidius.5.right, scalenus.dorsalis.left, scalenus.dorsalis.right, scalenus.medius.left, scalenus.medius.right, scalenus.ventralis.left, spinalis.cervicis.left
3	0.00282	sternum, hyoid, thyroid, ribs.right, omohyoideus.left, omohyoideus.right, scalenus.ventralis.right, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternooccipitalis.left, sternooccipitalis.right, sternothyroideus.left, sternothyroideus.right
4	0	cranium, C1, scapula.left, scapula.right, humerus.left, humerus.right, cleidocervicalis.left, cleidocervicalis.right, cleidomastoideus.left, cleidomastoideus.right, intertransversarii.dorsalis.1.left, intertransversarii.dorsalis.1.right, levator.claviculae.left, levator.claviculae.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, omotrachelian.left, omotrachelian.right, rectus.capitis.dorsalis.intermedius.left, rectus.capitis.dorsalis.intermedius.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, rhomboideus.capitis.left, rhomboideus.capitis.right
5	0.02777	ligamentum.nuchae, thoracic.spine, biventer.cervicis.left, biventer.cervicis.right, intertransversarii.dorsalis.7.left, intertransversarii.dorsalis.7.right, longissimus.capitis.left, longissimus.capitis.right, rhomboideus.cervicis.left, rhomboideus.cervicis.right, splenius.left, splenius.right, trapezius.left, trapezius.right

Table A25 Connectivity modules identified for *Giraffa camelopardalis*.

ID	p-value	Elements
1	0.03765	C2, C3, C4, longissimus.cervicis.left, longissimus.cervicis.right, longus.capitis.left, longus.capitis.right, longus.colli.left, longus.colli.right, omohyoideus.left, scalenus.ventralis.left, scalenus.ventralis.right, semispinalis.cervicis.left, interspinalis.1, interspinalis.2, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarius.dorsalis.2.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarius.dorsalis.2.right
2	0.00054	cranium, C1, biventer.cervicis.left, biventer.cervicis.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, splenius.capitis.left, splenius.capitis.right
3	0.07988	C7, thoracic.spine, nuchal.ligament, complexus.left, complexus.right, iliocostalis.cervicis.left, iliocostalis.cervicis.right, rhomboideus.cervicis.left, rhomboideus.cervicis.right, semispinalis.cervicis.right, trapezius.left, trapezius.right, interspinalis.5, interspinalis.6, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right
4	0.03006	C5, C6, scapula.left, scapula.right, humerus.left, humerus.right, cleidooccipitalis.left, cleidooccipitalis.right, longissimus.atlantis.left, longissimus.atlantis.right, longissimus.capitis.left, longissimus.capitis.right, omohyoideus.right, omotransversarius.left, omotransversarius.right, serratus.ventralis.cervicis.left, serratus.ventralis.cervicis.right, interspinalis.3, interspinalis.4, multifidius.submultifidius.4.left, intertransversarius.dorsalis.3.left, intertransversarius.dorsalis.4.left, intertransversarius.ventralis.longus.left, intertransversarius.ventralis.longus.right, multifidius.submultifidius.4.right, intertransversarius.dorsalis.3.right, intertransversarius.dorsalis.4.right
5	0.00023	mandible, sternum, hyoid, thyroid, ribs.left, ribs.right, scalenus.dorsalis.left, scalenus.dorsalis.right, scalenus.medius.left, scalenus.medius.right, scalenus.tertius.left, scalenus.tertius.right, sternomandibularis.left, sternomandibularis.right, sternothyrohyoideus.left, sternothyrohyoideus.right

Table A26 Connectivity modules identified for *Heteromys desmarestianus*.

ID	p-value	Elements
1	0.05536	C2, C3, C4, C5, intertransversarius.lateralis.longus.left, intertransversarius.lateralis.longus.right, longissimus.cervicis.left, longissimus.cervicis.right, longus.capitis.left, longus.capitis.right, rhomboideus.cervicis.left, rhomboideus.cervicis.right, scalenus.left, scalenus.right, semispinalis.cervicis.left, semispinalis.cervicis.right, serratus.ventralis.left, serratus.ventralis.right, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.3.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.3.right
2	0.37478	clavicle.right, scapula.right, acromiotrapezius.right, cleidomastoideus.right, cleidooccipitalis.right, omocervicalis.right, omohyoideus.right, rhomboideus.capitis.right
3	0.07763	C6, C7, thoracic.spine, iliocostalis.cervicis.left, iliocostalis.cervicis.right, longus.colli.left, longus.colli.right, semispinalis.capitis.left, semispinalis.capitis.right, splenius.left, splenius.right, multifidius.submultifidius.3.left, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.4.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, multifidius.submultifidius.3.right, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.4.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right
4	0.08267	sternum, ribs.left, ribs.right, longissimus.capitis.left, longissimus.capitis.right, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right
5	0.15519	clavicle.left, scapula.left, hyoid, thyroid, acromiotrapezius.left, cleidomastoideus.left, cleidooccipitalis.left, omocervicalis.left, omohyoideus.left, rhomboideus.capitis.left
6	0.00145	cranium, C1, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right

Table A27 Connectivity modules identified for *Homo sapiens*.

ID	p-value	Elements
1	0.02531	C6, C7, thoracic.spine, longissimus.capitis.left, longissimus.capitis.right, longus.colli.left, longus.colli.right, rhomboideus.minor.left, rhomboideus.minor.right, semispinalis.capitis.left, semispinalis.capitis.right, semispinalis.cervicis.left, spinalis.cervicis.left, spinalis.cervicis.right, interspinalis.5, interspinalis.6, multifidius.submultifidius.6.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, multifidius.submultifidius.6.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right
2	0.00423	C4, C5, ribs.left, ribs.right, iliocostalis.cervicis.left, iliocostalis.cervicis.right, longus.capitis.left, longus.capitis.right, scalenus.anticus.left, scalenus.anticus.right, scalenus.medius.left, scalenus.medius.right, scalenus.posticus.left, scalenus.posticus.right, interspinalis.3, interspinalis.4, multifidius.submultifidius.5.left, intertransversarius.dorsalis.3.left, intertransversarius.dorsalis.4.left, intertransversarius.ventralis.3.left, intertransversarius.ventralis.4.left, multifidius.submultifidius.5.right, intertransversarius.dorsalis.3.right, intertransversarius.dorsalis.4.right, intertransversarius.ventralis.3.right, intertransversarius.ventralis.4.right
3	0.03763	cranium, C1, nuchal.ligament, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, splenius.capitis.left, splenius.capitis.right, splenius.cervicis.left, splenius.cervicis.right, trapezius.left, trapezius.right
4	4e-05	clavicle.left, clavicle.right, scapula.left, scapula.right, sternum, hyoid, thyroid, omohyoideus.left, omohyoideus.right, sterno.cleido.mastoideus.left, sterno.cleido.mastoideus.right, sternohyoideus.left, sternohyoideus.right, sternothyroideus.left, sternothyroideus.right
5	0.12286	C2, C3, levator.scapulae.left, levator.scapulae.right, longissimus.cervicis.left, longissimus.cervicis.right, semispinalis.cervicis.right, interspinalis.1, interspinalis.2, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, multifidius.submultifidius.4.left, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.ventralis.1.left, intertransversarius.ventralis.2.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, multifidius.submultifidius.4.right, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right

Table A28 Connectivity modules identified for *Kogia breviceps*.

ID	p-value	Elements
1	0.03821	scapula.left, humerus.left, atlantoscapularis.ventralis.left, cleidomastoideus.left, rhomboideus.capitis.left
2	0.03821	scapula.right, humerus.right, atlantoscapularis.ventralis.right, cleidomastoideus.right, rhomboideus.capitis.right
3	0.00131	sternum, hyoid, thyroid, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right
4	0.00264	C2, C3, C4, longus.colli.left, spinalis.cervicis.left, spinalis.cervicis.right, interspinalis.1, interspinalis.2, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarius.dorsalis.2.left, intertransversarius.ventralis.2.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarius.dorsalis.2.right, intertransversarius.ventralis.2.right
5	1e-05	cranium, C1, ribs.left, ribs.right, longissimus.capitis.left, longissimus.capitis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, scalenus.dorsalis.left, scalenus.dorsalis.right, scalenus.medius.left, scalenus.medius.right, transversarius.capitis.left, transversarius.capitis.right
6	0.00235	C5, C6, longus.colli.right, interspinalis.3, interspinalis.4, interspinalis.5, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, intertransversarius.dorsalis.3.left, intertransversarius.dorsalis.4.left, intertransversarius.dorsalis.5.left, intertransversarius.ventralis.3.left, intertransversarius.ventralis.4.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, intertransversarius.dorsalis.3.right, intertransversarius.dorsalis.4.right, intertransversarius.ventralis.3.right, intertransversarius.ventralis.4.right
7	0.00086	C7, thoracic.spine, biventer.cervicis.left, biventer.cervicis.right, iliocostalis.capitis.left, iliocostalis.capitis.right, semispinalis.cervicis.left, semispinalis.cervicis.right, splenius.left, splenius.right, interspinalis.6, multifidius.submultifidius.6.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, multifidius.submultifidius.6.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right

Table A29 Connectivity modules identified for *Loris tardigradus*.

ID	p-value	Elements
1	0.06377	C2, C3, C4, longissimus.cervicis.left, longus.capitis.left, longus.capitis.right, longus.colli.left, scalenus.medius.left, scalenus.medius.right, semispinalis.cervicis.right, serratus.ventralis.cervicis.left, serratus.ventralis.cervicis.left.1, splenius.capitis.left, splenius.capitis.right, interspinalis.1, interspinalis.2, multifidius.submultifidius.1.left, multifidius.submultifidius.3.left, multifidius.submultifidius.4.left, intertransversarius.dorsalis.1.left, intertransversarius.ventralis.1.left, intertransversarius.ventralis.2.left, multifidius.submultifidius.1.right, multifidius.submultifidius.3.right, multifidius.submultifidius.4.right, intertransversarius.dorsalis.1.right, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right
2	0.00077	cranium, C1, clavicle.left, scapula.left, atlantoscapularis.anterior.left, cleidomastoideus.left, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, rhomboideus.capitis.left, trapezius.left
3	0.85385	C5, interspinalis.3, interspinalis.4, multifidius.submultifidius.2.left, multifidius.submultifidius.5.left, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.4.left, intertransversarius.ventralis.3.left, intertransversarius.ventralis.4.left, multifidius.submultifidius.2.right, multifidius.submultifidius.5.right, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.4.right, intertransversarius.ventralis.3.right, intertransversarius.ventralis.4.right
4	0.02154	C6, C7, thoracic.spine, complexus.left, complexus.right, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.right, longus.colli.right, rhomboideus.minor.left, rhomboideus.minor.right, semispinalis.cervicis.left, spinalis.cervicis.left, spinalis.cervicis.right, interspinalis.5, interspinalis.6, multifidius.submultifidius.6.left, intertransversarius.dorsalis.3.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, multifidius.submultifidius.6.right, intertransversarius.dorsalis.3.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right
5	0.35463	clavicle.right, scapula.right, atlantoscapularis.anterior.right, cleidomastoideus.right, omohyoideus.right, rhomboideus.capitis.right, trapezius.right
6	0.01359	sternum, hyoid, thyroid, ribs.left, ribs.right, iliocostalis.dorsalis.left, iliocostalis.dorsalis.right, omohyoideus.left, scalenus.posticus.left, scalenus.posticus.right, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right

Table A30 Connectivity modules identified for *Macaca mulatta*.

ID	p-value	Elements
1	0.00022	cranium, C1, clavicle.left, scapula.left, atlantoscapularis.anterior.left, atlantoscapularis.posterior.left, biventer.cervicis.left, biventer.cervicis.right, cleidomastoideus.left, cleidooccipitalis.left, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, rhomboideus.capitis.left, trapezius.left
2	0.00188	clavicle.right, scapula.right, sternum, hyoid, thyroid, atlantoscapularis.anterior.right, atlantoscapularis.posterior.right, cleidomastoideus.right, cleidooccipitalis.right, omohyoideus.left, omohyoideus.right, rhomboideus.capitis.right, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right, trapezius.right
3	0.85385	C2, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, rectus.capitis.dorsalis.major.left, interspinalis.1, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarius.dorsalis.1.left, intertransversarius.ventralis.1.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarius.dorsalis.1.right, intertransversarius.ventralis.1.right
4	0.13821	C6, C7, thoracic.spine, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.right, rhomboideus.minor.left, rhomboideus.minor.right, semispinalis.cervicis.left, semispinalis.cervicis.right, spinalis.cervicis.left, spinalis.cervicis.right, splenius.capitis.left, splenius.capitis.right, interspinalis.4, interspinalis.5, interspinalis.6, multifidius.submultifidius.6.left, intertransversarius.dorsalis.4.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.4.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, multifidius.submultifidius.6.right, intertransversarius.dorsalis.3.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right
5	0.01653	C3, C4, C5, complexus.left, complexus.right, longissimus.cervicis.left, longus.capitis.left, longus.capitis.right, longus.colli.left, longus.colli.right, scalenus.anticus.left, scalenus.anticus.right, serratus.ventralis.cervicis.left, serratus.ventralis.cervicis.left.1, interspinalis.2, interspinalis.3, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.3.left, intertransversarius.ventralis.2.left, intertransversarius.ventralis.3.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.4.right, intertransversarius.ventralis.2.right, intertransversarius.ventralis.3.right, intertransversarius.ventralis.4.right
6	0.84134	ribs.left, iliocostalis.dorsalis.left, scalenus.medius.left, scalenus.posticus.left
7	0.84134	ribs.right, iliocostalis.dorsalis.right, scalenus.medius.right, scalenus.posticus.right

Table A31 Connectivity modules identified for *Macropus rufus*.

ID	p-value	Elements
1	0.00655	C2, C3, C4, acromiotrachelien.left, longissimus.atlantis.left, longissimus.atlantis.right, longissimus.capitis.left, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, semispinalis.capitis.right, splenius.cervicis.left, splenius.cervicis.right, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarii.dorsalis.1.left, intertransversarii.dorsalis.2.left, intertransversarii.dorsalis.3.left, intertransversarii.ventralis.1.left, intertransversarii.ventralis.2.left, intertransversarii.ventralis.3.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarii.dorsalis.1.right, intertransversarii.dorsalis.2.right, intertransversarii.dorsalis.3.right, intertransversarii.ventralis.1.right, intertransversarii.ventralis.2.right, intertransversarii.ventralis.3.right
2	0.00039	cranium, C1, clavicle.right, scapula.right, nuchal.ligament, acromiotrachelien.right, atlantoscapularis.right, cleidomastoideus.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.dorsalis.superficialis.left, rectus.capitis.dorsalis.superficialis.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rhomboideus.left, rhomboideus.right, semispinalis.capitis.left, splenius.capitis.left, splenius.capitis.right, trapezius.right
3	0	C5, C6, C7, thoracic.spine, ribs.left, ribs.right, iliocostalis.dorsi.left, iliocostalis.dorsi.right, longissimus.capitis.right, longissimus.cervicis.left, longissimus.cervicis.right, longus.capitis.left, longus.capitis.right, longus.colli.left, longus.colli.right, scalenus.medius.left, scalenus.medius.right, scalenus.posticus.left, scalenus.posticus.right, serratus.magnus.right, interspinalis.6, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarii.dorsalis.4.left, intertransversarii.dorsalis.5.left, intertransversarii.dorsalis.6.left, intertransversarii.ventralis.4.left, intertransversarii.ventralis.5.left, intertransversarii.ventralis.6.left, spinalis.cervicis.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarii.dorsalis.4.right, intertransversarii.dorsalis.5.right, intertransversarii.dorsalis.6.right, intertransversarii.ventralis.4.right, intertransversarii.ventralis.5.right, intertransversarii.ventralis.6.right, spinalis.cervicis.right
4	0.00151	clavicle.left, scapula.left, sternum, hyoid, thyroid, atlantoscapularis.left, cleidomastoideus.left, omohyoideus.left, omohyoideus.right, serratus.magnus.left, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right, trapezius.left

Table A32 Connectivity modules identified for *Macrotis lagotis*.

ID	p-value	Elements
1	0.92103	C5, scalenus.posticus.left, interspinalis.3, interspinalis.4, multifidius.submultifidius.4.left, intertransversarii.dorsalis.3.left, intertransversarii.dorsalis.4.left, intertransversarii.ventralis.3.left, intertransversarii.ventralis.4.left, multifidius.submultifidius.4.right, intertransversarii.dorsalis.3.right, intertransversarii.dorsalis.4.right, intertransversarii.ventralis.3.right, intertransversarii.ventralis.4.right
2	0.95573	ribs.right, longus.colli.right, scalenus.medius.right, scalenus.posticus.right
3	0.00123	sternum, hyoid, thyroid, omohyoideus.left, omohyoideus.right, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right
4	0.01198	C6, C7, thoracic.spine, ribs.left, complexus.right, iliocostalis.dorsi.left, iliocostalis.dorsi.right, longissimus.capitis.left, longus.colli.left, scalenus.medius.left, semispinalis.cervicis.left, semispinalis.cervicis.right, splenius.capitis.left, splenius.capitis.right, splenius.cervicis.right, interspinalis.5, interspinalis.6, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarii.dorsalis.5.left, intertransversarii.dorsalis.6.left, intertransversarii.ventralis.5.left, intertransversarii.ventralis.6.left, spinalis.cervicis.left, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarii.dorsalis.5.right, intertransversarii.dorsalis.6.right, intertransversarii.ventralis.5.right, intertransversarii.ventralis.6.right
5	0.09181	C2, C3, C4, complexus.left, longissimus.capitis.right, longissimus.cervicis.left, longissimus.cervicis.right, rhomboideus.cervicis.left, serratus.magnus.left, serratus.magnus.right, splenius.cervicis.left, interspinalis.1, interspinalis.2, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarii.dorsalis.1.left, intertransversarii.dorsalis.2.left, intertransversarii.ventralis.1.left, intertransversarii.ventralis.2.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarii.dorsalis.1.right, intertransversarii.dorsalis.2.right, intertransversarii.ventralis.1.right, intertransversarii.ventralis.2.right, spinalis.cervicis.right
6	0.5	scapula.right, humerus.right, atlantoacromialis.right, atlantoscapularis.right, cleidooccipitalis.right, rhomboideus.capitis.right, rhomboideus.cervicis.right, trapezius.right
7	0.002	cranium, C1, scapula.left, humerus.left, atlantoacromialis.left, atlantoscapularis.left, biventer.cervicis.left, biventer.cervicis.right, cleidooccipitalis.left, longus.capitis.left, longus.capitis.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.dorsalis.superficialis.left, rectus.capitis.dorsalis.superficialis.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rhomboideus.capitis.left, trapezius.left

Table A33 Connectivity modules identified for *Manis pentadactyla*.

ID	p-value	Elements
1	0.20531	C2, C3, longus.capitis.right, rectus.capitis.dorsalis.major.right, scalenus.longus.left, scalenus.longus.right, serratus.ventralis.cervicis.left, serratus.ventralis.cervicis.right, splenius.capitis.right, interspinalis.1, interspinalis.2, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.ventralis.1.left, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.ventralis.1.right
2	0.20356	C6, C7, thoracic.spine, iliocostalis.cervicis.left, iliocostalis.cervicis.right, longissimus.cervicis.left, longissimus.cervicis.right, longus.colli.left, longus.colli.right, semispinalis.capitis.left, semispinalis.capitis.right, semispinalis.cervicis.left, semispinalis.cervicis.right, trapezius.left, interspinalis.5, interspinalis.6, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right
3	0.02714	C4, C5, longissimus.capitis.left, longissimus.capitis.right, longus.capitis.left, scalenus.brevis.left, scalenus.brevis.right, splenius.capitis.left, interspinalis.3, interspinalis.4, intertransversarius.dorsalis.3.left, intertransversarius.dorsalis.4.left, intertransversarius.ventralis.2.left, intertransversarius.ventralis.3.left, intertransversarius.ventralis.4.left, intertransversarius.dorsalis.3.right, intertransversarius.dorsalis.4.right, intertransversarius.ventralis.2.right, intertransversarius.ventralis.3.right, intertransversarius.ventralis.4.right
4	0.00082	sternum, hyoid, thyroid, ribs.left, ribs.right, tongue, sternoglossus.left, sternoglossus.right, sternohyoideus.left, sternohyoideus.right, sterno.mastoideus.left, sterno.mastoideus.right, sternothyroideus.left, sternothyroideus.right
5	6e-05	cranium, C1, humerus.left, humerus.right, scapula.left, scapula.right, cleidohumeralis.left, cleidohumeralis.right, levator.claviculae.left, levator.claviculae.right, mastoscapularis.left, mastoscapularis.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rhomboideus.capitis.left, rhomboideus.capiti.right, rhomboideus.cervicis.left, rhomboideus.cervicis.right, trapezius.right

Table A34 Connectivity modules identified for *Micropotamogale ruwenzorii*.

ID	p-value	Elements
1	4e-05	scapula.left, scapula.right, sternum, hyoid, thyroid, clavicula.left, clavicula.right, omocervicalis.left, omocervicalis.right, omohyoid.left, omohyoid.right, sternohyoid.left, sternohyoid.right, sternomastoideus.left, sternomastoideus.right, sternooccipitalis.left, sternothyroid.left, sternothyroid.right
2	0.00988	cranium, C1, biventer.cervicis.left, biventer.cervicis.left.1, longus.capitis.left, longus.capitis.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.lateralis.right.1, rectus.capitis.ventralis.left, rhomboideus.left, rhomboideus.right, sternooccipitalis.right, trapezius.left, trapezius.right
3	0.74307	C5, interspinalis.3, interspinalis.4, intertransversarius.dorsalis.3.left, intertransversarius.dorsalis.4.left, intertransversarius.ventralis.3.left, intertransversarius.ventralis.4.left, multifidius.submultifidius.4.right, intertransversarius.dorsalis.3.right, intertransversarius.dorsalis.4.right, intertransversarius.ventralis.3.right, intertransversarius.ventralis.4.right
4	0.00136	C2, C3, C4, ribs.left, ribs.right, iliocostalis.cervicis.left, iliocostalis.cervicis.right, scalenus.medius.left, scalenus.medius.right, scalenus.supracostalis.left, scalenus.supracostalis.right, serratus.ventralis.cervicis.left, serratus.ventralis.cervicis.right, interspinalis.1, interspinalis.2, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.ventralis.1.left, intertransversarius.ventralis.2.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right
5	0.03031	C6, C7, thoracic.spine, biventer.cervicis.right, biventer.cervicis.right.1, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.left, longissimus.cervicis.right, splenius.left, splenius.right, interspinalis.5, interspinalis.6, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right

Table A35 Connectivity modules identified for *Neotoma fuscipes*.

ID	p-value	Elements
1	7e-05	C5, C6, C7, thoracic.spine, acromiotrapezius.left, acromiotrapezius.right, semispinalis.capitis.left, semispinalis.capitis.right, serratus.ventralis.right, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.left, longissimus.cervicis.right, longus.colli.left, longus.colli.right, rhomboideus.anticus.right, splenius.left, splenius.right, semispinalis.cervicis.left, semispinalis.cervicis.right, interspinalis.4, interspinalis.5, interspinalis.6, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.4.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.4.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.4.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.4.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right
2	1e-05	cranium, C1, clavicle.left, clavicle.right, scapula.right, cleidomastoideus.left, cleidomastoideus.right, cleidotrapezius.left, cleidotrapezius.right, levator.claviculae.left, levator.claviculae.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.dorsalis.superficialis.left, rectus.capitis.dorsalis.superficialis.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, rhomboideus.capitis.right
3	0.04027	sternum, hyoid, thyroid, ribs.left, ribs.right, iliocostalis.cervicis.left, iliocostalis.cervicis.right, omohyoideus.right, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right
4	0.00199	C2, C3, C4, longus.atlantis.left, longus.atlantis.right, longus.capitis.left, longus.capitis.right, scalenus.anticus.left, scalenus.anticus.right, scalenus.medius.left, scalenus.medius.right, scalenus.tertius.left, scalenus.tertius.right, interspinalis.1, interspinalis.2, interspinalis.3, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.3.left, intertransversarius.ventralis.1.left, intertransversarius.ventralis.2.left, intertransversarius.ventralis.3.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.3.right, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right, intertransversarius.ventralis.3.right
5	0.92103	scapula.left, serratus.ventralis.left, omohyoideus.left, rhomboideus.anticus.left, rhomboideus.capitis.left

Table A36 Connectivity modules identified for *Notoryctes typhlops*.

ID	p-value	Elements
1	0.02926	cranium, C1, longus.capitis.left, longus.capitis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.dorsalis.superficialis.left, rectus.capitis.dorsalis.superficialis.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right
2	0.29166	clavicle.left, scapula.left, humerus.left, acromiotrapezius.left, cleidooccipitalis.left, omohyoideus.left, rhomboideus.left
3	0.03674	C2, C3, C4, complexus.left, complexus.right, longissimus.cervicis.left, longissimus.cervicis.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, scalenus.medius.left, scalenus.medius.right, splenius..left, splenius.right, interspinalis.1, interspinalis.2, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarii.dorsalis.1.left, intertransversarii.dorsalis.2.left, intertransversarii.ventralis.1.left, intertransversarii.ventralis.2.left, spinalis.cervicis.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarii.dorsalis.1.right, intertransversarii.dorsalis.2.right, intertransversarii.ventralis.1.right, intertransversarii.ventralis.2.right, spinalis.cervicis.right
4	0.00174	clavicle.right, scapula.right, sternum, hyoid, thyroid, humerus.right, cleidooccipitalis.right, omohyoideus.right, rhomboideus.right, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right
5	0.3078	C5, C6, scalenus.posticus.left, scalenus.posticus.right, semispinalis.cervicis.right, serratus.magnus.left, serratus.magnus.right, interspinalis.3, interspinalis.4, multifidius.submultifidius.4.left, multifidius.submultifidius.6.left, intertransversarii.dorsalis.3.left, intertransversarii.dorsalis.4.left, intertransversarii.dorsalis.5.left, intertransversarii.ventralis.3.left, intertransversarii.ventralis.4.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, intertransversarii.dorsalis.3.right, intertransversarii.dorsalis.4.right, intertransversarii.ventralis.3.right, intertransversarii.ventralis.4.right
6	0.09564	C7, thoracic.spine, ribs.left, ribs.right, acromiotrapezius.right, iliocostalis.dorsi.left, iliocostalis.dorsi.right, longissimus.capitis.left, longissimus.capitis.right, longus.colli.left, longus.colli.right, semispinalis.cervicis.left, interspinalis.5, interspinalis.6, multifidius.submultifidius.5.left, intertransversarii.dorsalis.6.left, intertransversarii.ventralis.5.left, intertransversarii.ventralis.6.left, multifidius.submultifidius.6.right, intertransversarii.dorsalis.5.right, intertransversarii.dorsalis.6.right, intertransversarii.ventralis.5.right, intertransversarii.ventralis.6.right

Table A37 Connectivity modules identified for *Ornithorhynchus anatinus*.

ID	p-value	Elements
1	0.15264	C2, C3, intertransversarii.dorsalis.cervicis.left, intertransversarii.dorsalis.cervicis.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, scalenus.left, scalenus.right, spinalis.cervicis.left, spinalis.cervicis.right, intertransversarius.ventralis.2.left, intertransversarius.ventralis.3.left, intertransversarius.ventralis.2.right, intertransversarius.ventralis.3.right
2	0.00021	C4, C5, C6, C7, thoracic.spine, complexus.major.left, complexus.major.right, iliocostalis.cervicis.left, iliocostalis.cervicis.right, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.left, longissimus.cervicis.right, longus.colli.left, longus.colli.right, rhomboideus.left, rhomboideus.right, serratus.ventralis.cervicis.left, serratus.ventralis.cervicis.right, splenius.left, splenius.right, intertransversarius.ventralis.4.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, intertransversarius.ventralis.7.left, intertransversarius.ventralis.4.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right, intertransversarius.ventralis.7.right
3	0.5	scapula.left, clavicula.left, levator.scapulae.dorsalis.left, levator.scapulae.ventralis.left, omohyoid.left, sterno.cleido.mastoid.left, trapezius.anterior.left
4	0.00196	scapula.right, sternum, hyoid, thyroid, ribs.left, ribs.right, clavicula.right, levator.scapulae.dorsalis.right, levator.scapulae.ventralis.right, omohyoid.right, sterno.cleido.mastoid.right, sternohyoid.left, sternohyoid.right, sternothyroid.left, sternothyroid.right, trapezius.anterior.right
5	0.06848	cranium, C1, biventer.cervicis.left, biventer.cervicis.right, longus.capitis.left, longus.capitis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.brevis.left, rectus.capitis.lateralis.brevis.right, rectus.capitis.lateralis.longus.left, rectus.capitis.lateralis.longus.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, intertransversarius.ventralis.1.left, intertransversarius.ventralis.1.right

Table A38 Connectivity modules identified for *Orycteropus afer*.

ID	p-value	Elements
1	0.03997	C6, C7, thoracic.spine, ribs.left, iliocostalis.cervicis.left, iliocostalis.cervicis.right, longissimus.cervicis.left, longissimus.cervicis.right, longus.colli.left, longus.colli.right, semispinalis.capitis.left, semispinalis.capitis.right, semispinalis.cervicis.left, semispinalis.cervicis.right, splenius.capitis.left, splenius.capitis.right, interspinalis.5, interspinalis.6, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right
2	1e-05	cranium, C1, clavicle.left, clavicle.right, scapula.left, scapula.right, nuchal.ligament, clavotrapezius.left, clavotrapezius.right, cleido.mastoideus.left, cleido.mastoideus.right, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.medius.left, rectus.capitis.dorsalis.medius.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rhomboideus.cervicis.left, rhomboideus.cervicis.right, trapezius.left, trapezius.right
3	0.06344	C4, C5, longissimus.capitis.left, longissimus.capitis.right, longus.capitis.left, scalenus.brevis.left, scalenus.brevis.right, serratus.ventralis.cervicis.left, interspinalis.3, interspinalis.4, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.3.left, intertransversarius.dorsalis.4.left, intertransversarius.ventralis.2.left, intertransversarius.ventralis.3.left, intertransversarius.ventralis.4.left, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.3.right, intertransversarius.dorsalis.4.right, intertransversarius.ventralis.3.right, intertransversarius.ventralis.4.right
4	0.00868	sternum, hyoid, thyroid, ribs.right, sternohyoideus.left, sternohyoideus.right, sterno.mastoideus.left, sterno.mastoideus.right, sternothyroideus.left, sternothyroideus.right
5	0.01016	C2, C3, levator.claviculae.left, levator.claviculae.right, levator.scapulae.left, levator.scapulae.right, longus.capitis.right, obliquus.capitis.caudalis.left, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, scalenus.longus.left, scalenus.longus.right, serratus.ventralis.cervicis.right, interspinalis.1, interspinalis.2, intertransversarius.dorsalis.1.left, intertransversarius.ventralis.1.left, intertransversarius.dorsalis.1.right, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right

Table A39 Connectivity modules identified for *Oryctolagus cuniculus*.

ID	p-value	Elements
1	0.08183	C2, C3, longus.capitis.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, rectus.capitis.dorsalis.superficialis.left, rhomboideus.right, semispinalis.capitis.right, splenius.left, splenius.right, trapezius.left, interspinalis.1, interspinalis.2, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.ventralis.1.left, intertransversarius.ventralis.2.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right
2	0.00124	sternum, hyoid, thyroid, ribs.left, iliocostalis.cervicis.left, scalenus.medius.left, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right
3	0	cranium, C1, humerus.left, humerus.right, scapula.left, scapula.right, cleidomastoideus.left, cleidomastoideus.right, cleidooccipitalis.left, cleidooccipitalis.right, levator.claviculae.left, levator.claviculae.right, levator.scapulae.left, levator.scapulae.right, longissimus.capitis.left, longissimus.capitis.right, longus.capitis.left, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.dorsalis.superficialis.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, semispinalis.capitis.left
4	0.05301	C4, C5, ribs.right, iliocostalis.cervicis.right, longus.atlantis.left, longus.atlantis.right, scalenus.anticus.left, scalenus.anticus.right, scalenus.medius.right, scalenus.tertius.left, scalenus.tertius.right, serratus.ventralis.left, serratus.ventralis.right, interspinalis.3, interspinalis.4, multifidius.submultifidius.3.left, multifidius.submultifidius.4.left, intertransversarius.dorsalis.3.left, intertransversarius.dorsalis.4.left, intertransversarius.ventralis.3.left, intertransversarius.ventralis.4.left, multifidius.submultifidius.3.right, multifidius.submultifidius.4.right, intertransversarius.dorsalis.3.right, intertransversarius.dorsalis.4.right, intertransversarius.ventralis.3.right, intertransversarius.ventralis.4.right
5	0.04779	C6, C7, thoracic.spine, longissimus.cervicis.left, longissimus.cervicis.right, longus.colli.left, longus.colli.right, rhomboideus.left, semispinalis.cervicis.left, semispinalis.cervicis.right, spinalis.cervicis.left, spinalis.cervicis.right, splenius.capitis.left, splenius.capitis.right, trapezius.right, interspinalis.5, interspinalis.6, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right

Table A40 Connectivity modules identified for *Pedetes capensis*.

ID	p-value	Elements
1	0.65572	clavicle.left, scapula.left, cleidomastoideus.left, cleidotrapezius.left, levator.claviculae.left, rhomboideus.anticus.left, trapezius.left
2	0.00014	cranium, C1, clavicle.right, scapula.right, cleidomastoideus.right, cleidotrapezius.right, levator.claviculae.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.dorsalis.superficialis.left, rectus.capitis.dorsalis.superficialis.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, rhomboideus.anticus.right, splenius.cervicis.left, splenius.cervicis.right, trapezius.right
3	0.01531	sternum, hyoid, thyroid, ribs.left, ribs.right, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right
4	0.01957	C6, C7, thoracic.spine, iliocostalis.cervicis.left, iliocostalis.cervicis.right, longissimus.cervicis.left, longissimus.cervicis.right, longus.colli.left, longus.colli.right, semispinalis.spinalis.cervicis.left, semispinalis.spinalis.cervicis.left.1, splenius.left, splenius.right, interspinalis.5, interspinalis.6, multifidius.submultifidius.3.left, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, multifidius.submultifidius.3.right, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right
5	0.02471	C2, C3, C4, longus.capitis.left, longus.capitis.right, scalenus.medius.left, scalenus.medius.right, scalenus.tertius.left, scalenus.tertius.right, semispinalis.capitis.left, semispinalis.capitis.right, serratus.ventralis.left, serratus.ventralis.right, interspinalis.1, interspinalis.2, multifidius.submultifidius.1.left, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.ventralis.1.left, intertransversarius.ventralis.2.left, multifidius.submultifidius.1.right, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right
6	0.5382	C5, interspinalis.3, interspinalis.4, multifidius.submultifidius.2.left, multifidius.submultifidius.4.left, intertransversarius.dorsalis.3.left, intertransversarius.dorsalis.4.left, intertransversarius.ventralis.3.left, intertransversarius.ventralis.4.left, multifidius.submultifidius.2.right, multifidius.submultifidius.4.right, intertransversarius.dorsalis.3.right, intertransversarius.dorsalis.4.right, intertransversarius.ventralis.3.right, intertransversarius.ventralis.4.right

Table A41 Connectivity modules identified for *Phascolarctos cinereus*.

ID	p-value	Elements
1	0	cranium, mandible, C1, clavicle.left, clavicle.right, scapula.left, scapula.right, sternum, ribs.right, atlantoscapularis.left, atlantoscapularis.right, biventer.cervicis.left, biventer.cervicis.right, cleidomastoideus.left, cleidomastoideus.right, cleidooccipitalis.left, cleidooccipitalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, omohyoideus.left, omohyoideus.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.dorsalis.superficialis.left, rectus.capitis.dorsalis.superficialis.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rhomboideus.left, rhomboideus.right, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, trapezius.left, trapezius.right
2	0.00236	C2, C3, C4, longissimus.cervicis.left, longus.capitis.left, longus.capitis.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, scalenus.posticus.left, scalenus.posticus.right, serratus.magnus.left, serratus.magnus.right, interspinalis.1, interspinalis.2, interspinalis.3, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarii.dorsalis.1.left, intertransversarii.dorsalis.2.left, intertransversarii.dorsalis.3.left, intertransversarii.ventralis.1.left, intertransversarii.ventralis.2.left, intertransversarii.ventralis.3.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarii.dorsalis.1.right, intertransversarii.dorsalis.2.right, intertransversarii.dorsalis.3.right, intertransversarii.ventralis.1.right, intertransversarii.ventralis.2.right, intertransversarii.ventralis.3.right
3	0.74991	ribs.left, iliocostalis.dorsi.right, longus.colli.right
4	2e-05	C5, C6, C7, thoracic.spine, complexus.left, complexus.right, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.right, scalenus.medius.left, scalenus.medius.right, semispinalis.cervicis.left, semispinalis.cervicis.right, splenius.capitis.left, splenius.capitis.right, splenius.cervicis.left, splenius.cervicis.right, interspinalis.4, interspinalis.5, interspinalis.6, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarii.dorsalis.4.left, intertransversarii.dorsalis.5.left, intertransversarii.dorsalis.6.left, intertransversarii.ventralis.4.left, intertransversarii.ventralis.5.left, intertransversarii.ventralis.6.left, spinalis.cervicis.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarii.dorsalis.4.right, intertransversarii.dorsalis.5.right, intertransversarii.dorsalis.6.right, intertransversarii.ventralis.4.right, intertransversarii.ventralis.5.right, intertransversarii.ventralis.6.right, spinalis.cervicis.right
5	0.87411	hyoid, thyroid, iliocostalis.dorsi.left, longus.colli.left, sternothyroideus.left, sternothyroideus.right

Table A42 Connectivity modules identified for *Procavia capensis*.

ID	p-value	Elements
1	0.00026	cranium, C1, scapula.left, humerus.left, brachiocephalicus.left, levator.claviculae.left, levator.scapulae.left, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rhomboideus.capitis.left, splenius.capitis.left, splenius.capitis.right, splenius.cervicis.left, splenius.cervicis.right, trapezius.left
2	0.40414	scapula.right, humerus.right, brachiocephalicus.right, levator.claviculae.right, levator.scapulae.right, rhomboideus.capitis.right, rhomboideus.cervicis.right, serratus.ventralis.right, trapezius.right
3	1e-04	mandible, sternum, hyoid, thyroid, cleidomastoideus.left, cleidomastoideus.right, sternohyoid.left, sternohyoid.right, sternomaxillaris.left, sternomaxillaris.right, sternothyroid.left, sternothyroid.right
4	0.06012	C2, C3, C4, complexus.major.left, complexus.tertius.left, complexus.tertius.right, longus.colli.left, longus.colli.right, rhomboideus.cervicis.left, interspinalis.1, interspinalis.2, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.ventralis.1.left, intertransversarius.ventralis.2.left, spinalis.cervicis.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right, spinalis.cervicis.right
5	0.0413	C5, C6, ribs.left, ribs.right, longus.capitis.left, longus.capitis.right, scalenus.anticus.left, scalenus.anticus.right, scalenus.posticus.left, scalenus.posticus.right, serratus.ventralis.left, interspinalis.3, interspinalis.4, multifidius.submultifidius.4.left, intertransversarius.dorsalis.3.left, intertransversarius.dorsalis.4.left, intertransversarius.ventralis.3.left, intertransversarius.ventralis.4.left, multifidius.submultifidius.4.right, intertransversarius.dorsalis.3.right, intertransversarius.dorsalis.4.right, intertransversarius.ventralis.3.right, intertransversarius.ventralis.4.right
6	0.15363	C7, thoracic.spine, complexus.major.right, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.left, longissimus.cervicis.right, interspinalis.5, interspinalis.6, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right

Table A43 Connectivity modules identified for *Pteropus vampyrus*.

ID	p-value	Elements
1	0	C5, C6, C7, thoracic.spine, levator.scapulae.left, levator.scapulae.right, scalenus.posterior.left, scalenus.posterior.right, semispinalis.capitis.left, semispinalis.capitis.right, semispinalis.cervicis.left, semispinalis.cervicis.right, splenius.capitis.left, splenius.capitis.right, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.4.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.4.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.4.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.4.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right
2	0.12745	cranium, C1, longus.capitis.left, longus.capitis.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, sternomastoideus.right
3	0.97939	ribs.left, scalenus.medius.left
4	3e-04	C2, C3, C4, cervico.clavicularis.left, cervico.clavicularis.right, intertransversus.lateralis.left, intertransversus.lateralis.right, longus.colli.left, longus.colli.right, scalenus.medius.right, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.3.left, intertransversarius.ventralis.1.left, intertransversarius.ventralis.2.left, intertransversarius.ventralis.3.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.3.right, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right, intertransversarius.ventralis.3.right
5	7e-05	clavicle.left, clavicle.right, scapula.left, scapula.right, sternum, hyoid, thyroid, ribs.right, cleidomastoideus.left, cleidomastoideus.right, omohyoideus.left, omohyoideus.right, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternothyroideus.left, sternothyroideus.right

Table A44 Connectivity modules identified for *Ptilocercus lowii*.

ID	p-value	Elements
1	0.04718	sternum, thyroid, ribs.left, ribs.right, scalenus.medius.left, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right
2	7e-04	C2, C3, C4, levator.anguli.scapulae.left, levator.anguli.scapulae.right, rectus.capitis.dorsalis.superficialis.left, rectus.capitis.dorsalis.superficialis.right, scalenus.medius.right, scalenus.posticus.left, scalenus.posticus.right, trapezius.right, interspinalis.1, interspinalis.2, interspinalis.3, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.3.left, intertransversarius.ventralis.1.left, intertransversarius.ventralis.2.left, intertransversarius.ventralis.3.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.3.right, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right, intertransversarius.ventralis.3.right
3	0.00011	C5, C6, C7, thoracic.spine, complexus.left, complexus.right, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.left, longissimus.cervicis.right, longus.capitis.left, longus.capitis.right, longus.colli.left, longus.colli.right, semispinalis.cervicis.left, semispinalis.cervicis.right, splenius.capitis.left, splenius.capitis.right, interspinalis.4, interspinalis.5, interspinalis.6, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.4.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.4.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.4.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.4.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right
4	0	cranium, C1, clavicle.left, clavicle.right, scapula.left, scapula.right, hyoid, cleidomastoideus.left, cleidomastoideus.right, cleidooccipitalis.left, cleidooccipitalis.right, levator.claviculae.left, levator.claviculae.right, levator.scapulae.left, levator.scapulae.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, omohyoideus.left, omohyoideus.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, rhomboideus.capitis.left, rhomboideus.capitis.right, trapezius.left

Table A45 Connectivity modules identified for *Sarcophilus harrisii*.

ID	p-value	Elements
1	1e-05	C5, C6, C7, thoracic.spine, ribs.left, complexus.left, iliocostalis.dorsi.left, longissimus.capitis.left, longissimus.capitis.right, longus.colli.left, rhomboideus.left, rhomboideus.right, scalenus.posticus.left, semispinalis.cervicis.left, semispinalis.cervicis.right, serratus.magnus.left, serratus.magnus.right, interspinalis.4, interspinalis.5, interspinalis.6, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarii.dorsalis.4.left, intertransversarii.dorsalis.5.left, intertransversarii.dorsalis.6.left, intertransversarii.ventralis.4.left, intertransversarii.ventralis.5.left, intertransversarii.ventralis.6.left, spinalis.cervicis.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarii.dorsalis.4.right, intertransversarii.dorsalis.5.right, intertransversarii.dorsalis.6.right, intertransversarii.ventralis.4.right, intertransversarii.ventralis.5.right, intertransversarii.ventralis.6.right, spinalis.cervicis.right
2	0.09383	cranium, C1, longus.capitis.left, longus.capitis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.dorsalis.superficialis.left, rectus.capitis.dorsalis.superficialis.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, splenius..left, splenius.right
3	0.0071	sternum, hyoid, thyroid, omohyoideus.left, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right
4	0.14549	clavicle.right, scapula.right, humerus.right, atlantoscapularis.dorsalis.right, atlantoscapularis.right, cleidomastoideus.right, omohyoideus.right, rhomboideus.capitis.right, trapezius.right
5	0.19186	clavicle.left, scapula.left, humerus.left, atlantoscapularis.dorsalis.left, atlantoscapularis.left, cleidomastoideus.left, rhomboideus.capitis.left, trapezius.left
6	0.00064	C2, C3, C4, complexus.right, longissimus.cervicis.left, longissimus.cervicis.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, scalenus.medius.left, scalenus.medius.right, interspinalis.1, interspinalis.2, interspinalis.3, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarii.dorsalis.1.left, intertransversarii.dorsalis.2.left, intertransversarii.dorsalis.3.left, intertransversarii.ventralis.1.left, intertransversarii.ventralis.2.left, intertransversarii.ventralis.3.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarii.dorsalis.1.right, intertransversarii.dorsalis.2.right, intertransversarii.dorsalis.3.right, intertransversarii.ventralis.1.right, intertransversarii.ventralis.2.right, intertransversarii.ventralis.3.right
7	0.97573	ribs.right, iliocostalis.dorsi.right, longus.colli.right, scalenus.posticus.right

Table A46 Connectivity modules identified for *Scalopus aquaticus*.

ID	p-value	Elements
1	0.00031	C2, C3, C4, longissimus.capitis.left, longissimus.capitis.right, longus.atlantis.left, longus.atlantis.right, longus.colli.left, longus.colli.right, scalenus.b.left, scalenus.b.right, splenius.left, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.3.left, intertransversarius.ventralis.1.left, intertransversarius.ventralis.2.left, intertransversarius.ventralis.3.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.3.right, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right, intertransversarius.ventralis.3.right
2	0	cranium, C1, clavicle.left, clavicle.right, scapula.left, scapula.right, cleido.mastoideus.left, cleido.mastoideus.right, cleido.occipitalis.left, cleido.occipitalis.right, levator.claviculae.left, levator.claviculae.right, levator.scapulae.left, levator.scapulae.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, rhomboideus.capitis.left, rhomboideus.capitis.right
3	0.0055	sternum, hyoid, thyroid, ribs.left, ribs.right, scalenus.a.left, scalenus.a.right, sternohyoideus.left, sternohyoideus.right, sterno.mastoideus.left, sterno.mastoideus.right, sterno.occipitalis.left, sterno.occipitalis.right, sternothyroideus.left, sternothyroideus.right
4	0.00013	C5, C6, C7, thoracic.spine, longissimus.cervicis.left, longissimus.cervicis.right, longus.capitis.left, longus.capitis.right, rhomboideus.cervicis.left, rhomboideus.cervicis.right, semispinalis.capitis.left, semispinalis.capitis.right, semispinalis.cervicis.left, semispinalis.cervicis.right, serratus.ventralis.cervicis.left, serratus.ventralis.cervicis.right, splenius.right, trapezius.anticus.left, trapezius.anticus.right, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.4.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.4.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.4.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.4.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right

Table A47 Connectivity modules identified for *Sciurus vulgaris*.

ID	p-value	Elements
1	1e-05	cranium, C1, C2, scapula.left, biventer.cervicis.left, biventer.cervicis.right, levator.claviculae.left, levator.scapulae.left, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.dorsalis.superficialis.left, rectus.capitis.dorsalis.superficialis.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, rhomboideus.capitis.left, rhomboideus.left, splenius.left, splenius.right, trapezius.left, interspinalis.1, multifidius.submultifidius.1.left, intertransversarius.dorsalis.1.left, intertransversarius.ventralis.1.left, multifidius.submultifidius.1.right, intertransversarius.dorsalis.1.right, intertransversarius.ventralis.1.right
2	0	C6, C7, thoracic.spine, ribs.left, ribs.right, complexus.left, complexus.right, iliocostalis.cervicis.left, iliocostalis.cervicis.right, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.left, longissimus.cervicis.right, longus.atlantis.d.left, longus.atlantis.d.right, scalenus.tertius.left, scalenus.tertius.right, semispinalis.cervicis.left, semispinalis.cervicis.right, spinalis.cervicis.left, spinalis.cervicis.right, splenius.capitis.left, splenius.capitis.right, interspinalis.5, interspinalis.6, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right
3	0.00056	C3, C4, C5, longus.atlantis.v.left, longus.atlantis.v.right, longus.capitis.left, longus.capitis.right, longus.colli.left, longus.colli.right, scalenus.anticus.left, scalenus.anticus.right, scalenus.medius.left, scalenus.medius.right, serratus.ventralis.left, interspinalis.2, interspinalis.3, interspinalis.4, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, multifidius.submultifidius.4.left, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.3.left, intertransversarius.dorsalis.4.left, intertransversarius.ventralis.2.left, intertransversarius.ventralis.3.left, intertransversarius.ventralis.4.left, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, multifidius.submultifidius.4.right, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.3.right, intertransversarius.dorsalis.4.right, intertransversarius.ventralis.2.right, intertransversarius.ventralis.3.right, intertransversarius.ventralis.4.right
4	0.89312	scapula.right, levator.claviculae.right, levator.scapulae.right, omohyoideus.right, rhomboideus.capitis.right, rhomboideus.right, serratus.ventralis.right, trapezius.right
5	0.00061	clavicle.left, clavicle.right, sternum, hyoid, thyroid, cleidomastoideus.left, cleidomastoideus.right, cleidooccipitalis.left, cleidooccipitalis.right, omohyoideus.left, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right

Table A48 Connectivity modules identified for *Suncus murinus*.

ID	p-value	Elements
1	0.00539	C2, C3, C4, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, scalenus.b.left, splenius.left, splenius.right, trapezius.anticus.left, trapezius.anticus.right, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.3.left, intertransversarius.ventralis.1.left, intertransversarius.ventralis.2.left, intertransversarius.ventralis.3.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.3.right, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right, intertransversarius.ventralis.3.right
2	0.95246	ribs.right, iliocostalis.cervicis.left.1, scalenus.a.right, scalenus.b.right
3	0.97033	ribs.left, iliocostalis.cervicis.left, scalenus.a.left
4	0.11436	C1, longus.colli.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right
5	5e-05	C5, C6, C7, thoracic.spine, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.left, longissimus.cervicis.right, longus.colli.left, rhomboideus.cervicis.left, rhomboideus.cervicis.right, semispinalis.capitis.left, semispinalis.capitis.right, serratus.ventralis.cervicis.left, serratus.ventralis.cervicis.right, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.4.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.4.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.4.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.4.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right
6	0	cranium, clavicle.left, clavicle.right, scapula.left, scapula.right, sternum, hyoid, thyroid, cleido.mastoideus.left, cleido.mastoideus.right, cleido.occipitalis.left, cleido.occipitalis.right, levator.claviculae.left, levator.claviculae.right, longus.capitis.left, longus.capitis.right, rhomboideus.capitis.left, rhomboideus.capitis.right, sternohyoideus.left, sternohyoideus.right, sterno.mastoideus.left, sterno.mastoideus.right, sternothyroideus.left, sternothyroideus.right, trapezius.capitis.left, trapezius.capitis.right

Table A49 Connectivity modules identified for *Tachyglossus aculeatus*.

ID	p-value	Elements
1	0.7044	scapula.left, clavicula.left, levator.scapulae.dorsalis.left, levator.scapulae.ventralis.left, trapezius.anterior.left
2	0.3559	C3, C4, C5, intertransversarii.dorsalis.cervicis.left, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.left, longissimus.cervicis.right, obliquus.capitis.caudalis.right, scalenus.left, scalenus.right, serratus.ventralis.cervicis.left, serratus.ventralis.cervicis.right, intertransversarius.ventralis.3.left, intertransversarius.ventralis.4.left, intertransversarius.ventralis.3.right, intertransversarius.ventralis.4.right
3	0.00035	sternum, hyoid, thyroid, ribs.left, ribs.right, omohyoid.left, omohyoid.right, sterno.cleido.mastoid.left, sterno.cleido.mastoid.right, sternoglossus.left, sternoglossus.right, sternothyroid.left, sternothyroid.right, tongue
4	0.58505	scapula.right, clavicula.right, levator.scapulae.dorsalis.right, levator.scapulae.ventralis.right, trapezius.anterior.right
5	0.15295	C6, C7, thoracic.spine, complexus.major.left, complexus.major.right, iliocostalis.cervicis.left, iliocostalis.cervicis.right, longus.colli.left, longus.colli.right, rhomboideus.left, rhomboideus.right, spinalis.cervicis.left, spinalis.cervicis.right, splenius.left, splenius.right, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, intertransversarius.ventralis.7.left, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right, intertransversarius.ventralis.7.right
6	0.00175	cranium, C1, C2, biventer.cervicis.left, biventer.cervicis.right, intertransversarii.dorsalis.cervicis.right, longus.capitis.left, longus.capitis.right, obliquus.capitis.caudalis.left, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.brevis.left, rectus.capitis.lateralis.brevis.right, rectus.capitis.lateralis.longus.left, rectus.capitis.lateralis.longus.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right, intertransversarius.ventralis.1.left, intertransversarius.ventralis.2.left, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right

Table A50 Connectivity modules identified for *Tapirus indicus*.

ID	p-value	Elements
1	0.00021	mandible, scapula.right, sternum, hyoid, thyroid, ribs.left, ribs.right, omohyoideus.right, scalenus.1st.rib.right, scalenus.medius.left, scalenus.medius.right, scalenus.transcostalis.left, scalenus.transcostalis.right, sternohyoideus.left, sternohyoideus.right, sternomandibularis.left, sternomandibularis.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right
2	0.0018	C5, C6, C7, levator.scapulae.left, levator.scapulae.right, longissimus.cervicis.left, longissimus.cervicis.right, longus.capitis.left, longus.capitis.right, scalenus.1st.rib.left, semispinalis.capitis.b.left, semispinalis.capitis.b.right, spinalis.cervicis.left, spinalis.cervicis.right, interspinalis.4, interspinalis.5, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.4.left, intertransversarius.dorsalis.5.left, intertransversarius.ventralis.4.left, intertransversarius.ventralis.5.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.4.right, intertransversarius.dorsalis.5.right, intertransversarius.ventralis.4.right, intertransversarius.ventralis.5.right
3	0.01125	thoracic.spine, nuchal.ligament, rhomboideus.cervicis.left, rhomboideus.cervicis.right, semispinalis.capitis.a.left, semispinalis.capitis.a.right, splenius.left, splenius.right, trapezius.left, trapezius.right, interspinalis.6, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.6.left, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.6.right
4	0.00821	C2, C3, C4, iliocostalis.cervicis.left, iliocostalis.cervicis.right, longus.colli.left, longus.colli.right, interspinalis.1, interspinalis.2, interspinalis.3, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.3.left, intertransversarius.ventralis.2.left, intertransversarius.ventralis.3.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.3.right, intertransversarius.ventralis.2.right, intertransversarius.ventralis.3.right
5	0.00272	cranium, C1, humerus.right, brachiocephalicus.a.right, brachiocephalicus.b.right, longissimus.capitis.left, longissimus.capitis.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right
6	0.41123	scapula.left, humerus.left, brachiocephalicus.a.left, brachiocephalicus.b.left, omohyoideus.left

Table A51 Connectivity modules identified for *Trichosurus vulpecula*.

ID	p-value	Elements
1	0.01524	mandible, sternum, thyroid, ribs.left, ribs.right, iliocostalis.dorsi.left, iliocostalis.dorsi.right, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right
2	0	cranium, C1, clavicle.left, clavicle.right, scapula.left, scapula.right, hyoid, atlantoscapularis..ventralis.right, atlantoscapularis.dorsalis.left, atlantoscapularis.dorsalis.right, atlantoscapularis.ventralis.left, biventer.cervicis.left, biventer.cervicis.right, cleidomastoideus.left, cleidomastoideus.right, cleidooccipitalis.left, cleidooccipitalis.right, longissimus.capitis.left, longissimus.capitis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, omohyoideus.left, omohyoideus.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rhomboideus.right, splenius.right
3	0.00022	C5, C6, C7, thoracic.spine, complexus.left, complexus.right, lo.cer..iliocostalis.cervicis..left, lo.cer..iliocostalis.cervicis..right, longus.colli.left, longus.colli.right, scalenus.medius.left, scalenus.medius.right, serratus.magnus.left, serratus.magnus.right, trapezius.left, trapezius.right, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarii.dorsalis.4.left, intertransversarii.dorsalis.5.left, intertransversarii.dorsalis.6.left, intertransversarii.ventralis.4.left, intertransversarii.ventralis.5.left, intertransversarii.ventralis.6.left, spinalis.cervicis.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarii.dorsalis.4.right, intertransversarii.dorsalis.5.right, intertransversarii.dorsalis.6.right, intertransversarii.ventralis.4.right, intertransversarii.ventralis.5.right, intertransversarii.ventralis.6.right, spinalis.cervicis.right
4	0.00392	C2, C3, C4, longus.capitis.left, longus.capitis.right, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, rhomboideus.left, scalenus.posticus.left, scalenus.posticus.right, splenius.left, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarii.dorsalis.1.left, intertransversarii.dorsalis.2.left, intertransversarii.dorsalis.3.left, intertransversarii.ventralis.1.left, intertransversarii.ventralis.2.left, intertransversarii.ventralis.3.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarii.dorsalis.1.right, intertransversarii.dorsalis.2.right, intertransversarii.dorsalis.3.right, intertransversarii.ventralis.1.right, intertransversarii.ventralis.2.right, intertransversarii.ventralis.3.right

Table A52 Connectivity modules identified for *Vespertilio murinus*.

ID	p-value	Elements
1	4e-05	clavicle.left, clavicle.right, scapula.left, scapula.right, sternum, hyoid, thyroid, cervico.clavicularis.left, cervico.clavicularis.right, cleidomastoideus.left, cleidomastoideus.right, omohyoideus.left, omohyoideus.right, sternohyoideus.left, sternohyoideus.right, sternomastoideus.left, sternomastoideus.right, sternothyroideus.left, sternothyroideus.right
2	0.01239	C2, C3, C4, longus.capitis.left, longus.capitis.right, longus.colli.left, longus.colli.right, splenius.capitis.left, splenius.capitis.right, multifidius.submultifidius.1.left, multifidius.submultifidius.2.left, multifidius.submultifidius.3.left, intertransversarius.dorsalis.1.left, intertransversarius.dorsalis.2.left, intertransversarius.dorsalis.3.left, intertransversarius.ventralis.1.left, intertransversarius.ventralis.2.left, intertransversarius.ventralis.3.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.right, multifidius.submultifidius.3.right, intertransversarius.dorsalis.1.right, intertransversarius.dorsalis.2.right, intertransversarius.dorsalis.3.right, intertransversarius.ventralis.1.right, intertransversarius.ventralis.2.right, intertransversarius.ventralis.3.right
3	0	C5, C6, C7, thoracic.spine, ribs.left, ribs.right, levator.scapulae.left, levator.scapulae.right, scalenus.medius.left, scalenus.medius.right, scalenus.posterior.left, scalenus.posterior.right, semispinalis.capitis.left, semispinalis.capitis.right, semispinalis.cervicis.left, semispinalis.cervicis.right, multifidius.submultifidius.4.left, multifidius.submultifidius.5.left, multifidius.submultifidius.6.left, intertransversarius.dorsalis.4.left, intertransversarius.dorsalis.5.left, intertransversarius.dorsalis.6.left, intertransversarius.ventralis.4.left, intertransversarius.ventralis.5.left, intertransversarius.ventralis.6.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.right, multifidius.submultifidius.6.right, intertransversarius.dorsalis.4.right, intertransversarius.dorsalis.5.right, intertransversarius.dorsalis.6.right, intertransversarius.ventralis.4.right, intertransversarius.ventralis.5.right, intertransversarius.ventralis.6.right
4	0.00071	cranium, C1, longissimus.capitis.left, longissimus.capitis.right, obliquus.capitis.caudalis.left, obliquus.capitis.cranialis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right

Table A53 Connectivity modules identified for *Zalophus californianus*.

ID	p-value	Elements
1	0.00749	sternum, hyoid, thyroid, ribs.left, omohyoideus.left, omohyoideus.right, scalenus.dorsalis.left, scalenus.medius.left, sternomastoideus.left, sternomastoideus.right, sternothyrohyoideus.left, sternothyrohyoideus.right
2	0.8807	ribs.right, scalenus.dorsalis.right, scalenus.medius.right
3	0.03134	ligamentum.nuchae, scapula.left, scapula.right, humerus.left, humerus.right, cleidocervicalis.left, cleidocervicalis.right, cleidomastoideus.left, cleidomastoideus.right, humerotrapezius.left, humerotrapezius.right, levator.scapula.1.left, levator.scapula.1.right, levator.scapula.2.left, levator.scapula.2.right, rhomboideus.capitis.left, rhomboideus.capitis.right, rhomboideus.cervicis.left, rhomboideus.cervicis.right, splenius.left, splenius.right
4	2e-05	C2, C3, C4, complexus.left, complexus.right, interspinalis.1, interspinalis.2, interspinalis.3, intertransversarii.dorsalis.2.left, intertransversarii.dorsalis.2.right, intertransversarii.dorsalis.3.left, intertransversarii.dorsalis.3.right, intertransversarii.dorsalis.4.left, intertransversarii.dorsalis.4.right, intertransversarii.ventralis.left, intertransversarii.ventralis.right, intertransversarius.intermedius.1.left, intertransversarius.intermedius.1.right, intertransversarius.intermedius.2.left, intertransversarius.intermedius.2.right, intertransversarius.intermedius.3.left, intertransversarius.intermedius.3.right, levator.scapula.3.left, levator.scapula.3.right, longus.capitis.right, multifidius.submultifidius.1.left, multifidius.submultifidius.1.right, multifidius.submultifidius.2.left, multifidius.submultifidius.2.right, multifidius.submultifidius.3.left, multifidius.submultifidius.3.right, scalenus.ventralis.left, scalenus.ventralis.right
5	0.00594	cranium, C1, intertransversarii.dorsalis.1.left, intertransversarii.dorsalis.1.right, longus.capitis.left, obliquus.capitis.caudalis.left, obliquus.capitis.caudalis.right, obliquus.capitis.cranialis.left, obliquus.capitis.cranialis.right, rectus.capitis.dorsalis.major.left, rectus.capitis.dorsalis.major.right, rectus.capitis.dorsalis.minor.left, rectus.capitis.dorsalis.minor.right, rectus.capitis.lateralis.left, rectus.capitis.lateralis.right, rectus.capitis.ventralis.left, rectus.capitis.ventralis.right
6	0	C5, C6, C7, thoracic.spine, interspinalis.4, interspinalis.5, intertransversarii.dorsalis.5.left, intertransversarii.dorsalis.5.right, intertransversarii.dorsalis.6.left, intertransversarii.dorsalis.6.right, intertransversarii.dorsalis.7.left, intertransversarii.dorsalis.7.right, intertransversarius.intermedius.4.left, intertransversarius.intermedius.4.right, longissimus.capitis.left, longissimus.capitis.right, longissimus.cervicis.left, longissimus.cervicis.right, longus.colli.left, longus.colli.right, multifidius.submultifidius.4.left, multifidius.submultifidius.4.right, multifidius.submultifidius.5.left, multifidius.submultifidius.5.right, semispinalis.capitis.left, semispinalis.capitis.right, serratus.ventralis.cervicis.left, serratus.ventralis.cervicis.right, spinalis.cervicis.left, spinalis.cervicis.right, splenius.cervicis.left, splenius.cervicis.right

Musculoskeletal networks reveal topological disparity in mammalian neck evolution

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Additional file AF2_references

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Table A54 Systematics and references of investigated species

Higher Taxon	Order	Family	Species	Predatory behavior	References
Afrotheria	Afrosoricida	Chrysochloridae	*Chrysospalax trevelyani*	P	[1-4]
		Potamogalidae	*Micropotamogale ruwenzorii*	P	[4-7]
	Hyracoidea	Procaviidae	*Procavia capensis*	N	[7-10]
	Proboscidea	Elephantidae	*Elephas maximus*	N	[11-13]
	Sirenia	Dugongidae	*Dugong dugon*	N	[14, 15]
	Tubulidentata	Orycteropodidae	*Orycteropus afer*	N	[7, 16-20]
Euarchonta	Lagomorpha	Leporidae	*Oryctolagus cuniculus*	N	[21-24]
	Primates	Cercopithecidae	*Macaca mulatta*	N	[25-28]
		Hominidae	*Homo sapiens*	N	[29, 30]
		Lorisidae	*Loris tardigradus*	N	[31-34]
	Rodentia	Chinchillidae	*Chinchilla lanigera*	N	[35-38]
		Cricetidae	*Neotoma fuscipes*	N	[22, 39, 40]
		Heteromyidae	*Heteromys desmarestianus*	N	[22, 41]
		Pedetidae	*Pedetes capensis*	N	[42]
		Sciuridae	*Sciurus vulgaris*	N	[21, 36, 43, 44]
	Scandentia	Ptilocercidae	*Ptilocercus lowii*	P	[45-48]
Laurasiatheria	Carnivora	Canidae	*Canis lupus*	P	[49-51]
		Felidae	*Felis silvestris*	P	[52-54]
		Mustelidae	*Galictis cuja*	P	[55, 56]
		Otariidae	*Zalophus californianus*	P	[57, 58]
		Viverridae	*Civettictis civetta*	P	[51, 59-62]
	Cetartiodactyla	Bovidae	*Bos taurus*	N	[63-66]
		Camelidae	*Camelus bactrianus*	N	[9, 67]
		Giraffidae	*Giraffa camelopardalis*	N	[68-72]
		Kogiidae	*Kogia breviceps*	P	[73-77]
		Suidae	*Babyrousa babyrussa*	N	[78-80]
	Chiroptera	Pteropodidae	*Pteropus vampyrus*	N	[81, 82]
		Vespertilionidae	*Vespertilio murinus*	P	[81, 83]
	Eulipotyphla	Erinaceidae	*Erinaceus europaeus*	P	[4, 84, 85]
		Soricidae	*Suncus murinus*	P	[4, 84, 86-89
		Talpidae	*Scalopus aquaticus*	P	[4, 89-92]
	Perissodactyla	Equidae	*Equus caballus*	N	[93-95]
		Tapiridae	*Tapirus indicus*	N	[9, 10, 96]
	Pholidota	Manidae	*Manis pentadactyla*	N	[20, 97-99]
Marsupialia	Dasyuromorpha	Dasyuridae	*Sarcophilus harrisii*	P	[100-104]
	Didelphimorphia	Didelphidae	*Didelphis virginiana*	P	[105-108]
	Diprotodontia	Macropodidae	*Macropus rufus*	N	[109-112]
		Phalangeridae	*Trichosurus vulpecula*	N	[113-115]
		Phascolarctidae	*Phascolarctos cinereus*	N	[114-118]
	Notoryctemorphia	Notoryctidae	*Notoryctes typhlops*	P	[119-121]
	Paucituberculata	Caenolestidae	*Caenolestes fuliginosus*	P	[122]
	Peramelemorphia	Thylacomyidae	*Macrotis lagotis*	P	[123-125]

Higher Taxon	Order	Family	Species	Predatory behavior	References
Monotremata	Monotremata	Ornithorhynchidae	*Ornithorhynchus anatinus*	P	[108, 126-131]
		Tachyglossidae	*Tachyglossus aculeatus*	N	[127-129, 132-134]
Xenarthra	Cingulata	Dasypodidae	*Dasypus novemcinctus*	P	[20, 135-138
	Pilosa	Bradypodidae	*Bradypus tridactylus*	N	[20, 98, 139-141]
		Cyclopedidae	*Cyclopes didactylus*	N	[20, 98, 136, 142]
		Megalonychidae	*Choloepus didactylus*	N	[20, 98, 141, 143, 144]

Footnote: references also includes those ones for closely related species for which anatomical information were available to asses topological variation within the lineage

P: predatory; N: non-predatory

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Musculoskeletal networks reveal topological disparity in mammalian neck evolution

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Additional file AF3_methods

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Anatomical definitions

Muscles

We defined cervical muscles as muscles that originate from the cervical vertebrae, the skull (cranium or mandible), the nuchal ligament, or the hyoid/thyroid and insert on the (cervical or thoracic) vertebrae, sternum, pectoral girdle (scapulae, claviculae, humeri), or ribs. The definition includes:

- accessory field muscles (trapezius, sterno-cleido-cephalic, and their derivatives)
- dorsoscapular muscles (cervical and capital parts of rhomboid, atlantoscapularis, serratus ventralis, and their derivatives)
- prevertebral muscles (longus capitis and colli)
- long infrahyoid muscles (sternohyoid, sternothyroid, and omohyoid)
- cervical costal muscles (scaleni, intertransversarii ventralis, and their derivatives)
- transversospinal muscles (semispinalis capitis and cervicis, multifidi and their derivatives)
- sacrospinal muscles (cervical and capital parts of the longissimus, intertransversarii dorsalis and medialis, cervical and capital parts of the iliocostalis, and their derivatives)
- spinalis muscles (cervical spinalis and interspinalis)
- spinotransversal muscles (splenius capitis and cervicis)
- suboccipital muscles (rectus capitis dorsalis major, dorsalis minor, intermdius, lateralis, and ventralis and oblique capitis cranialis and caudalis)

The long infrahyoid muscles (sterno-, thyro- and omohyoid) were included as they act synergistic during head/neck motion [1, 2]. They were also closely related to the neck complex in an earlier study [3]. The thyrohoid muscle, in contrast, is excluded here as it is integrated in the laryngeal complex [3]. In cases in which the arrangement of the small intervertebral muscles (interspinalis, intertransversarii, multifidi) are not reported in detail, the descriptions of the large scale comparative works were used [4-6].

Bones and ligaments

Although consisting of several bones, the cranium, thoracic spine, left/right ribs, and hyoid were represented by only one element, respectively, to capture that their internal movements are not part of the head/neck motion. The nuchal ligament was only included if it was present as a distinct structure (e.g., when funicular and lamellar portions are present) rather than only by a nuchal raphe. Taxa in which the claviculae are either absent, reduced, intra-muscular or without physical connection to the sternum were treated as aclaviculate. Their cleidocephalic and clavo-deltoid muscles form a single functional unit connecting the cranium with the humeri (i.e., cephalo-humeral muscles).

Community structure and modularity

The community structure of an anatomical network is a hypothesis of modularity of their anatomical elements based on their structural relations, which can be caused by or affect to developmental, geometric and functional relations among parts (Esteve-Altava et al. 2013). A network module (or *community*) is a group of nodes highly connected among them and poorly connected to nodes in other groups. Finding the best partition of a medium-large network into modules is an NP-complete problem. For this reason community detection algorithms use heuristic approaches to find the best partition into modules (Fortunato 2010).

We used a spin-glass model and simulated annealing algorithm to identify the modules of the network. In this model, each node can be in one of *c* partitions, and the links between nodes specify which pairs of nodes would prefer to stay in the same module (because Q is higher) and which ones prefer to have different module (because Q is lower). The model is then simulated for a given number of steps. In the first steps, the algorithm is allowed, with more frequency, to accept partitions that are worse (lower Q) than our current partition. This gives the algorithm the ability to jump out of any local optimums it finds itself in early on in execution. Each successive step, this frequency of accepting worst partitions decreases, allowing the algorithm to gradually focus in on a area of the search space in which hopefully, a close to optimum solution can be found. For each network the algorithm is iterated 100 times and we take the consensus result, i.e., present most frequently.

We measured the *modularity* (Q) as defined by Newman and Girvan (2004) for the resulting modular organization of every method. The expected error on Q has been calculated using a jackknife procedure where every link is an independent observation, as suggested in (Newman and Girvan 2004). According to these authors, if the number of connections within modules is no better than random, Q will be close to 0; the higher the Q the stronger the modular organization of the network (maximum, Q=1); in practice, strongly modular networks show Q vales ranging from 0.3 to 0.7. Therefore, we consider that an anatomical network has a strong modular structure if $Q - error \geq 0.3$. The expected error on Q can be calculated using a jackknife procedure, where every link is an independent observation.

Complementarly, we evaluated the statistical significance of every module independently using a two-sample Wilcoxon rank-sum test on the *internal* and *external* connections of the module. According to the general definition of module as a group of nodes highly connected among them and poorly connected to nodes in other groups, we expect internal connections to be significatively higher than external connections. Thus,

- Ho: internal degree = external degree
- Ha: internal degree > external degree

A low *p-value* tells us to reject Ho, and hence we can assume the alternative hypothesis that the nodes of the module are more connected among them than to other nodes outside the module. In other words, the module identified is not expected by a random grouping of nodes.

Finally, to compare the degree of modularity among different anatomical networks we calculate the Parcellation index.

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Supplementary Material of Chapter 4

Mammalian Hox code and morphological modularity: homeotic transformations explain departure from mammalian ‘rule of seven’ in sloths

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SUPPLEMENTARY INFORMATION

Böhmer et al. "*Hox code* and morphological modularity: homeotic transformations explain departure from the mammalian 'rule of seven' in sloths"

<u>Content:</u>

Figure S1: Relative warps (RW) analysis results of interspecific dataset.

Figure S2: Results of cluster analysis for each specimen.

Figure S3: 3D renderings of all analyzed vertebrae.

Figure S4: Landmark set used in the 3D geometric morphometric analysis.

Table S1: Percentage of total variance explained and cumulative variance per relative warp (RW).

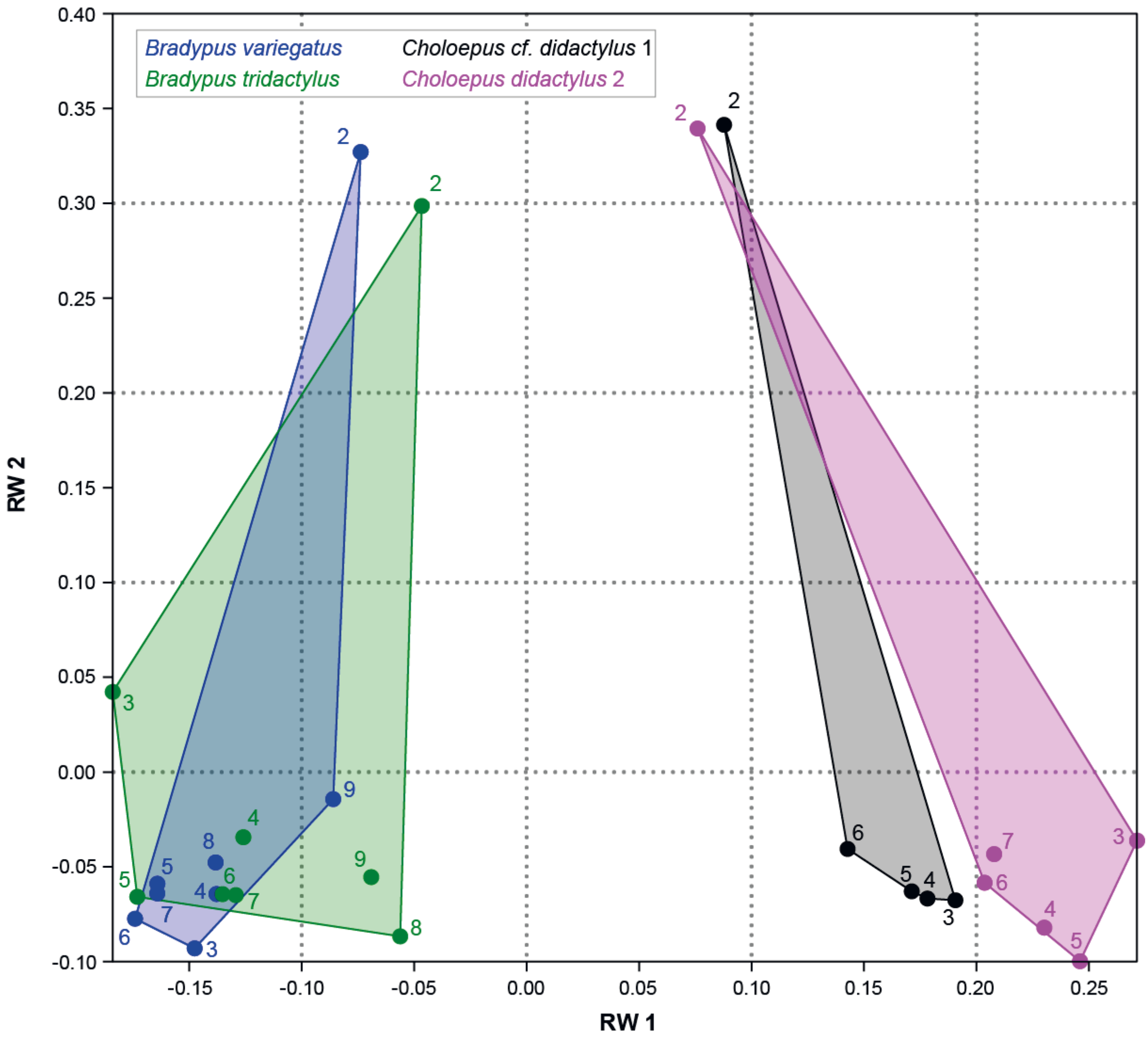

Fig. S1: Relative warps (RW) analysis results of interspecific dataset. The plot shows that the two genera *Choloepus* and *Bradypus* occupy distinct regions of the morphospace. *B. variegatus* and *B. tridactylus* cluster together, whereas the two specimens, *C. didactylus* do so as well but show less overlap. In all analyzed sloths, the C2 is very distinct in its morphology and is separate from the postaxial vertebrae.

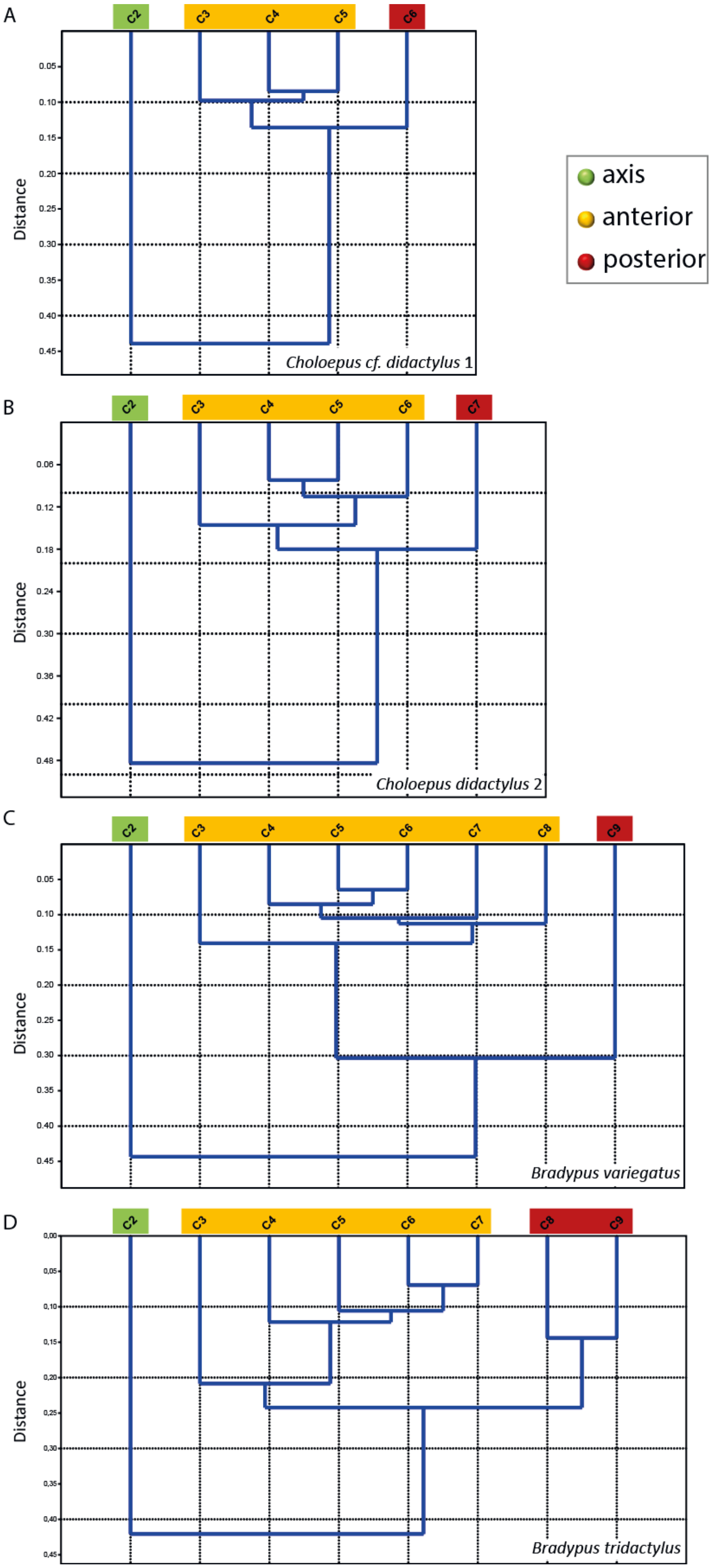

Fig. S2: Results of cluster analysis for each specimen. A three subunit pattern was revealed in all specimens analyzed. Green, axis; yellow, anterior subunit; red, posterior subunit. A, *C. cf. didactylus* 1; B, *C. didactylus* 2; C, *B. variegatus*; D, *B. tridactylus*.

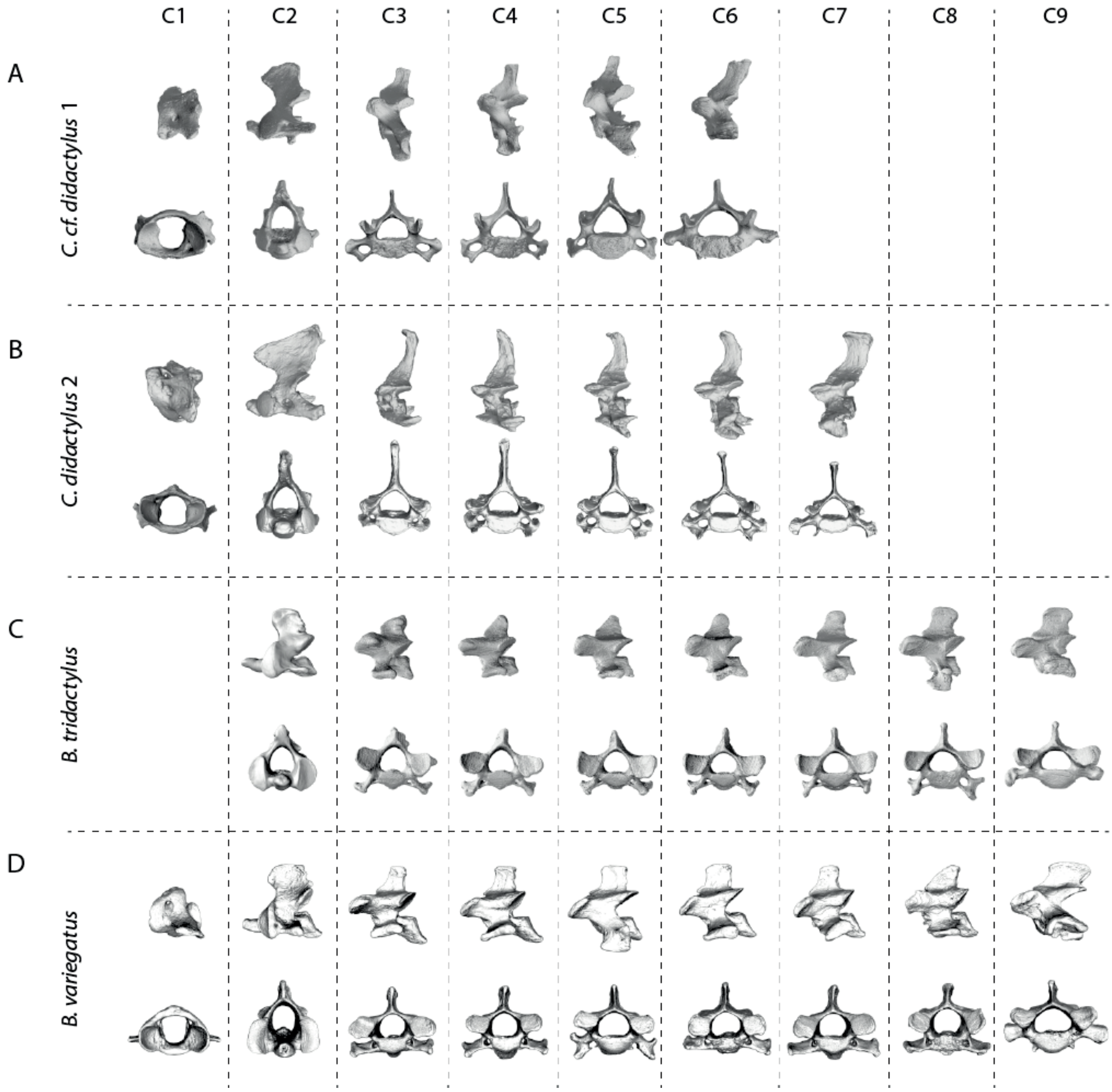

Fig. S3: 3D renderings of all analyzed vertebrae. For each specimen left lateral view above and anterior view below. A, *C. cf. didactylus* 1; B, *C. didactylus* 2; C, *B. variegatus*; D, *B. tridactylus*. C1 (atlas) of *B. tridactylus* was not available with the museum specimen. Note that the present analysis involved only postatlantal CV.

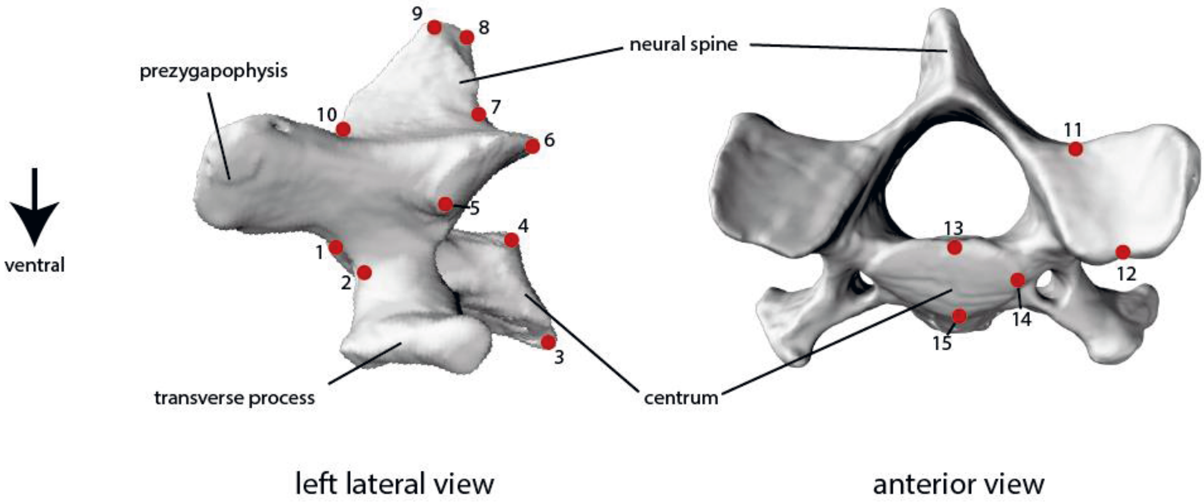

Fig. S4: Landmark set used in the 3D geometric morphometric analysis. The numbered 3D landmarks (red points) are shown on a mid-cervical vertebra of *Bradypus tridactylus* (3D model). LM1=dorsal-anterior edge of vertebral centrum, LM2=ventral-anterior edge of vertebral centrum, LM3=ventral-posterior edge of vertebral centrum, LM4=dorsal-posterior edge of vertebral centrum, LM5=anteriormost edge of articular facet of postzygapophysis, LM6=dorsal-posterior edge of articular facet of postzygapophysis, LM7=point of maximum curvature between postzygapophysis and neural spine, LM8=posterior edge of neural spine, LM9=anterior edge of neural spine, LM10=point of maximum curvature between neural spine and prezygapophysis, LM11=posteriormost point of articular facet of prezygapophysis, LM12=dorsal-anterior edge of articular facet of prezygapophysis, LM13=dorsalmost point of vertebral centrum in anterior view, LM14=lateralmost point of vertebral centrum in anterior view, LM15=ventralmost point of vertebral centrum in anterior view.

Table S1: Percentage of total variance explained and cumulative variance per relative warp (RW). Only the first four RWs are indicated since they explain more than 95% of the total variance.

	Variance [%]	**Cumulative variance [%]**
Choloepus cf. didactylus 1		
RW1	85.47	85.47
RW2	9.93	95.40
RW3	2.81	98.21
RW4	1.79	100.00
Choloepus didactylus 2		
RW1	82.66	82.66
RW2	9.09	91.75
RW3	4.85	96.60
RW4	2.09	98.69
Bradypus variegatus		
RW1	59.44	59.44
RW2	28.98	88.42
RW3	6.07	94.49
RW4	2.49	96.98
Bradypus tridactylus		
RW1	55.33	55.33
RW2	25.73	81.06
RW3	10.71	91.77
RW4	4.24	96.01